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MORPHOLOGICAL AND BIOLOGICAL NOTES ON NEW AND LITTLE KNOWN WEST-HIMALAYAN LIVERWORTS. III.

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[With Seven Figures in the Text.]

ROM what has been said in my two earlier papers¹ it will be seen that the process of reduction in the Marchantiales, so far as the gametophyte is concerned apart from the modification in the structure of the thallus, consists in the greater development of the vegetative tissue at the expense of the sex organs. This has taken place in two ways, resulting in two series of forms pretty distinct from each other.

- (1) By decrease in the number of branches of the female receptacle as indicated by the involucres, along with the elimination of the stalk of the carpocephalum. This is shown in the series: Exormotheca, Aitchisoniella and Targionia.
- (2) By decrease in the number of archegonia in each involucre until only one is found in each. The stalk is retained. In most cases the number of involucres in the carpocephalum is normally four or more. This is seen in the Astroporæ and Operculatæ of Leitgeb. In both series the greater development of the vegetative tissue is also manifest in the continued growth of the thallus after the formation of terminal carpocephala as seen in Stephensoniella and Plagiochasma articulatum. The sterilisation of some branches of the receptacles is also very conspicuous in the male receptacles of Cyathodium tuberosum and the female receptacles of Aitchisoniella, and a little less so in the female receptacle of Exormotheca.

The reason for this greater development of vegetative tissue and gradual reduction of the gametophores is to be found in the fact
1 NEW PHYTOLOGIST, Vol. 13, 1914, pp. 206-226, 308-323.

that these plants have adopted a xerophilous mode of life which is not suitable for their mode of sexual reproduction, as water is essential for this purpose. That they are xerophilous is shown by the many adaptations to enable them to pass through a dry period enumerated in the list given in the beginning of these notes. Only 2 species out of the 27 thallose liverworts found by the writer at Mussoorie are (doubtfully) annual—a species of Anthoceros and a species of Notothylas. All the Marchantiales can persist and what is more important do persist throughout the dry period in one way or another. This discontinuance of sexual reproduction may in its turn have led to reduction in the thallus and the sporophyte.

I now go on to describe some other interesting forms met with in the same region.

CRYPTOMITRIUM HIMALAYENSE KASHYAP, N.SP. (Fig. 1).

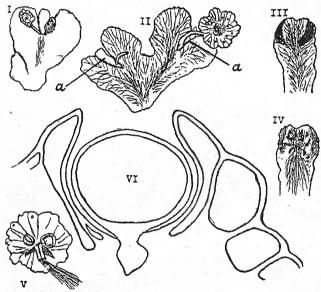
Plants monœcious, yellowish green, creeping, attached to the substratum along the narrow midrib only, or attached only at the base, once or twice forked. Lobes up to 6 mm. long, 6 to 7 mm. broad, midrib narrow, wings thin broad, margin irregularly and bluntly crenate. Apex cordate. Dorsal surface areolated; stomata slightly raised, in a few areoles only, one in each, surrounded by three rings of eight hyaline cells each. Air-chambers in one layer only, having only a single layer of cells above and below (roof and floor) throughout the broad wings. Scales minute, hyaline or greenish, ovate, distant, in two rows, margin of scale toothed occasionally, apex with a filament of 5 or 6 cells, cells of scale contain chloroplasts.

Antheridia in the median dorsal groove 2- or 3-seriate behind the female receptacle and on an adjacent lobe which does not form a female receptacle. Papillæ very small, inconspicuous.

Female receptacle usually on one lobe of a fork. Stalk with one deep groove, up to 3 mm. long and with 6 to 8 ridges. Receptacle thin, broad, circular with irregularly toothed margin, slightly convex in the centre, margin in the ripe state very often curved upwards. Stomata barrel-shaped. Involucres 2 to 4, most often 3, archegonia 2 in each. Sporogonia 1 to 3, foot and seta small, capsule wholly included. Operculum 600μ in diameter, definite, 2-layered; annulus cells 20 to 25μ in diameter; cells of capsule wall 50 to $80\mu \times 20\mu$. Spores brown, 55 to 60μ , broadly reticulate-lamellate, border hyaline. Elaters 350 to 400μ , closely trispiral.

The plant is interesting on account of its peculiar habitat and consequent modification of thallus structure and the possession of

apical tuber-like organs. It occurs in the deep shade of densely growing trees, or rocks, or in caves where its only companion is Cyathodium tuberosum. The latter may also occur in comparatively exposed places, but the present species never does. Consequently it has the yellowish colour of Cyathodium and similarly reduced thallus. The number of stomata is very small and as stated above the broad wings consist only of two layers of cells separated by air chambers. Both kinds of rhizoids are, however, present. The scales, like those of Cyathodium, contain chloroplasts. The rhizoid



Cryptomitrium himalayense. I, II, two fertile plants, I showing two young sporogonia, II showing a carpocephalum and also the position of the antheridia (a, a), \times 3. III, a lobe of the thallus from above—the apex is being cut off, \times 3. IV, the same, from below, \times 3. V, female receptacle seen from below, two involucres out of the four are fertile, x 4. VI, horizontal section of involucre with a sporogonium, x 50.

furrow is always one and never two as found by Stephani1 in some specimens of C. tenerum. At the end of the vegetative season the apex of the plant becomes condensed, the scales are nearer each other and scattered on the ventral surface, and the midrib is broader and thicker. The ventral surface and the scales assume a red colour, and soon two broad red curved bands appear on the dorsal side a little behind the apex one from each margin. They are concave anteriorly and ultimately meet in the centre. In this way a reniform area at the apex (Fig. 1, III, IV) becomes sharply marked off from the rest of the thallus, which later on gradually

^{1 &}quot;Species Hepaticarum," Vol. I, p. 148.

dies away. The margins of the apical portion bend upwards and become variously bent and twisted, so that the apical portion forms an irregular reddish knot when dry, but it opens out on moistening and begins to grow again. The twisting of the wings to form an irregular knot is very different from the mere rolling upwards of the margins as seen in *Plagiochasma*, etc.

FOSSOMBRONIA HIMALAYENSIS KASHYAP, N.SP. (Fig. 2).

Plants cæspitose among grass or moss, or singly on rocks, small and compact in the former places, but open and longer in the latter; two to three times branched, branches up to 6 mm. long. Rhizoids violet or hyaline. Leaves oblong, wavy, ascending, overlapping to about one-third of the length, outer margin irregularly and indistinctly toothed.



Fig. 2. Fossombronia himalayensis. I, a plant with two branches $(t, old\ tuber; t^l, tubers of current year), <math>\times$ 4. II, perianth with sporogonium, \times 4.

Monœcious or diœcious. Perianth with a wavy margin, sometimes split to the base along one side. Seta up to 5 mm. long, often very short; capsule usually exserted. Spores with furcate high lamellæ sometimes forming a few reticulations, 40 to 50μ . Elaters laxly bi- or trispiral, 100 to 140μ long. The cells of the outer layer of capsule wall have thin walls. No trace of bands was found as described by Humphrey in F. longiseta (Annals of Botany, Vol. 20, 1906). The cells of the inner layer have U-shaped bands on the inner and radial walls near the apex, but only simple bands on radial walls at other places. Dehiscence by separation of the apical portion.

At the end of the vegetative season the apex grows down into the soil and becomes thickened, as is the case in *F. tuberifera* described by Goebel ("Organography of Plants," Vol. 2, p. 68). Sometimes the tuber is almost sessile, but often it is borne on a long portion of the stem which forms only rudimentary leaves in the form of ridges. This portion of the stem may be up to 3 mm. in length and usually has a distinct spiral twist which helps the tuber in

New and Little Known West-Himalayan Liverworts. 5

burrowing down into the soil. The tuber has minute purple scales at the anterior extremity and is covered with rhizoids.

In the formation of the tubers this plant resembles F. tuberifera, but in the sculpture of the spores it is like F. cristata Lindb.

The cells of the stem contain some fungal hyphæ, but there is no definite mycorrhizal zone.

SEWARDIELLA KASHYAP, N.GEN. (Fig. 3).

Plants dieccious, thallose, simple or the wingless apical part of stem once forked, usually in thick patches on rocks or singly among mosses and grass, in shady places, up to 10 mm. long and 12 mm. broad; midrib thick projecting ventrally, rounded below. Ventral surface often with minute red scales in two rows. Wings often unequal many-layered at base, gradually becoming thin, one-layered throughout the greater portion, ascending, margins wavy; upper surface of thallus concave.

Male and female plants similar. Antheridia in a cluster on the dorsal surface on the midrib (Fig. 3, II, III), 12 to 24 in a cluster; each antheridium globular on a short multicellular stalk, not at all sunk in a pit; bracts a few scattered between the antheridia irregularly, simple or more or less deeply lobed (Fig. 3, XII-XIV). Archegonia in a cluster of about a dozen on the dorsal surface on the midrib. Perianth bell-shaped, margin lacerated into numerons narrow processes, often split in one or more places up to the base (Fig. 3, IX), many layered at base, one-layered above. Calyptra thin, one-layered. Sporogonia 1 to 3 in each perianth; foot small; seta up to 1.25 mm. long; capsule 1 to 1.3 mm. in diameter, included or slightly exerted. Capsule wall 2 or 3-layered, the cells of the outer layer usually thin walled, sometimes with thick bands on the radial walls, cells of inner layer with U-shaped bands on inner and radial walls or only simple bands on radial walls. Spores reticulatelamellate, less than four reticulations in the diameter, 40µ. Elaters bi- or trispiral, 300 to 400μ ; no fixed elaters at the base or elsewhere.

Species one—S. tuberifera; characters as above.

This plant is practically a thallose Fossombronia, in which the antheridia are formed in groups instead of being scattered.

As described above the wings are sometimes unequal even in the ripe plant. The anterior margin of one wing in the young state covers the anterior margin of the other while the posterior margin of the former is covered by the posterior margin of the latter. In the young state the wings are bent strongly upwards so

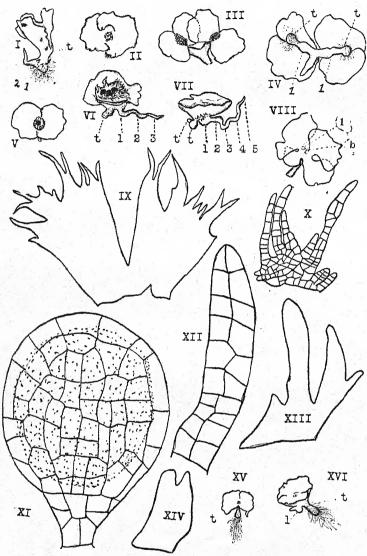


FIG. 3. Sewardiella tuberifera. I, a young plant in side view \times 2. II, a simple male plant showing antheridia and bracts, \times 2. III, a forked male plant, \times 2. IV, the same from below, \times 2. V, a female plant, with sporogonium, \times 2. VI, a female plant with three sporogonia within the perianth. VII, a plant in side view, showing scales and two young tubers at the apex, \times 2. VIII, a plant branched rather early (l, one rudimentary inner wing; b, bract). IX, perianth split open and spread out, \times 50; the split in the middle is natural. X, beginning of perianth formation—the entire young perianth showing bracts in various stages, \times 200. XI, an antheridium, \times 200. XII—XIV, male bracts, \times 200. XV, prothallus of Gymnogramme leptophylla, surface view. \times 2. XVI, the same, side view, \times 2. In all cases t=the current year's tubers; 1, 2, 3, etc., indicate tubers 1, 2, 3, etc., years old.

that they form a funnel; when the plant is mature and the wings are large they may hang down. In the young state the plant resembles the prothallus of Gymnogramme leptophylla very much. The prothallus is often found growing near the plant and it is impossible to distinguish the two in the young sterile state (cf. Fig. 3, I-VIII, XV-XVI). The cells of the midrib are full of starch especially in the central portion. The cells near the ventral surface and to the sides contain some fungal hyphæ. Near the end of the vegetative season the growing point ceases to form wings and only produces the cylindrical midrib. The apex then becomes thickened and forms a tuber which is covered with rhizoids and also some minute scales anteriorly, and it is buried in the soil. When the tuber grows next year the scales are carried to the ventral surface of the plant. Sometimes the wingless apex forks into two before forming a tuber and thus two tubers may be found in front of one plant. Rarely the forking may affect the wings as well. The plant shown in Fig. 3, VIII, looks as if there are two leaves on each side of the stem; as a matter of fact the apex has forked rather early and each branch has formed a wing on its outer side, but the wing on the inner side is as yet not developed—a rudiment of one of these inner wings is seen at l. Sometimes when the plant has forked, a wing may be developed on the dorsal side anteriorly between the two tubers and this wing may be more or less fused with the lateral wings and the three form a cup-like structure. As the plant goes on growing for several years forming one or two tubers each year, one often sees the remains of several years' tubers behind the current year's growth. Fig. 3, VII, shows a plant five years old. The up and down curves indicating yearly growth and the swellings indicating the position of the successive tubers are quite distinct.

The perianth arises in the form of several distinct bracts (Fig. 3, X), which, moreover, do not grow simultaneously. Each bract arises from a single cell as a small papilla which divides by transverse walls and forms a short filament. Then vertical walls are formed in the lower portion and as the bracts become broader the adjacent ones fuse and are then carried upwards by basal growth. Sometimes fusion can not take place at one or two places because the bracts are at a distance from each other, then the perianth in the ripe state shows some splits. As the bracts do not arise in a regular ring, but some towards the outside and others towards the centre nearer the archegonia, we find that in the ripe perianth the bracts may sometimes be fused to the inner and the outer surfaces.

Sometimes the number of these bracts is so great that the perianth has the appearance of a double flower.

This plant is extremely interesting in another way also. As pointed out above it is closely related to Fossombronia. There is no evidence to show whether the foliose form has arisen from the thallose form or vice versâ. The aggregation of the antheridia into a cluster, the scattered male bracts and the mode of development of the perianth seem to show that in the Jungermanniales also the thallose forms may have been derived from the foliose forms by reduction.

ANTHOCEROS HIMALAYENSIS KASHYAP, N.SP. (Fig. 4).

Plants diccious, closely attached to the substratum, green, black when dry, usually in large patches among moss or on earth. Dorsal surface with a midrib. Ventral surface with numerous rhizoids full of a granular substance stained brown with iodine.

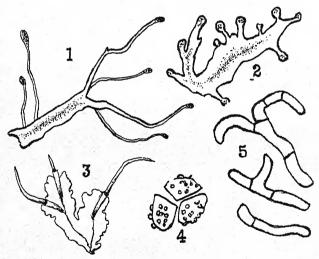


Fig. 4. Anthocoros himalayensis. 1, 2, sterile plants with tubers, \times 5; 3, female plant with young sporogonia, \times 3; 4, spores, \times 300; 5, elaters, \times 300. Margins raised slightly except in sterile plants. Sterile plants (Fig. 4, 1, 2) long linear forked 5 mm. or more long and 1 mm. broad, bearing tubers at the apex, on the margins or ventral surface. Tubers also sometimes on male and female plants.

Male plants smaller than female and less divided. Antheridia globose yellow, up to six in each chamber, usually three.

Female plants large, circular up to 20 mm. in diameter, deeply lobed, the lobes again with divided margins, lobes overlapping. Involucres often fused in pairs, cylindrical, slightly narrowed above,

mouth usually truncate or indistinctly irregularly toothed, surface smooth, up to 5 mm. long. Sporogonium stout, cylindrical, obtuse, up to 30 mm. long, with stomata on the wall. Spores (Fig. 4, 4), yellow, tetrahedral, convex surface with small round papillæ, 25μ . Pseudo-elaters (Fig. 4, 5) thin walled, branched, occasionally some simple, 10μ broad.

The tubers are sometimes embedded in the thallus. Usually they arise on long cylindrical stalks from the ventral surface or from the margins. The stalk may be up to 3 mm. long and the tuber up to 0.5 mm. in diameter. If the plants are growing among dense grass the tubers are mostly marginal and shortly stalked. Both the stalk and the tuber have some rhizoids. The tuber has a covering of empty cells. On pressing the tuber a milky fluid comes out. The germination of the tuber is exactly like that of A. phymatodes as figured by Howe ("The Hepaticæ and Anthocerotes of California," 1899). The old dry stalk is often seen on one side of the tuber.

ANTHOCEROS ERECTUS KASHYAP, N.SP. (Fig. 5).

Plants diœcious, in dense clusters on damp earth. Thallus thick, fleshy, often raised on a stalk-like underground structure and expanding above into a more or less cup-like body (Fig. 5, 1 to 3), sometimes branched from the very base (Fig. 5, 4, 5). Stalk usually tapers downwards, sometimes it is thickened at the lower end and is in any case covered with the rhizoids only at this end. Rhizoids full of a granular matter stained brown with iodine. The stalk and the thallus contain large chambers full of mucilage. The body of the thallus with a circular slightly toothed margin, or deeply divided into lobes, up to about 1 cm. in diameter.

Male plants smaller. Antheridia yellow when ripe, up to eight in each chamber. Involucres often fused in pairs, about 5 mm. long. Involucre-wall contains numerous mucilage chambers (Fig. 5, 7). Sporogonia (Fig. 5, 6) slender, acute, up to 30 mm. long, wall with stomata. Spores black granulose 30 to 40μ . Pseudo-elaters simple or branched (Fig. 5, 8).

The plant is interesting on account of its peculiar habit. It is often raised on a distinct stalk, the base of which may be either thick or pointed. It is, moreover, one of the only two thallose liverworts met with at Mussoorie which seem to be annual; the other is a species of Notothylas The plants only grow for three months (July to September), and then disappear. Another interesting point about the species of Anthoceros is that the rhizoids are not hyaline,

3

at least not always. I have observed this in the two species described here and in a third unidentified species from the plains. In all cases they were filled with minute granules which stain brown with iodine; I have never seen this appearance in any other liverwort.

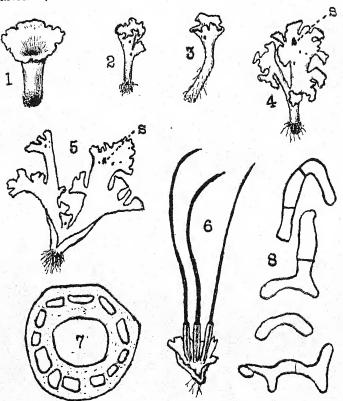


Fig. 5. Anthocoros erectus. 1, a sterile plant, \times 5; 2, 3, male plants with Nostoc colonies, \times 4; 4, 5, female plants with Nostoc colonies and young sporogonia at s, \times 4; 6, a lobe with three ripe sporogonia, \times 3; 7, transverse section of involucre, \times 70; 8, pseudo-elaters, \times 300.

ATHALAMIA PINGUIS FALC. (Fig. 6).

The genus Athalamia was founded by Dr. Hugh Falconer, Superintendent of the Calcutta Botanic Garden, to include a plant discovered by him and described in the Transactions of the Linnean Society (Vol. XX, 1851). The description, however, was very brief and mainly dealt with the external characters of the plant. Schiffner, therefore, in the "Natürliche Pflanzenfamilien," placed it as a doubtful genus at the end of the group Marchantioideæ-Astroporæ. He, however, says that "the genus is doubtless related to Clevea" and then within brackets he adds "or perhaps identical with Aytonia."

A plant has been found by the writer in Mussoorie which is undoubtedly the Athalamia pinguis of Falconer, and its further study has shown that Schiffner's first conjecture is right and that the plant is very closely related to Clevea. Falconer had only ripe plants which were beginning to wither and this was one reason why he could not make out several points. There can be no doubt about the identity of the plant after comparing it with Falconer's figures and his description.

The plant is one of the commonest liverworts in Mussoorie, and grows in dense patches on more or less exposed eastern slopes. The thallus is closely creeping on the earth or on the almost bare rock. It may remain simple or fork once or twice. The lobes are broad and do not diverge from one another, for which reason Falconer described the plant as radiately 3-lobed. The thallus is light green, fleshy, with a thick midrib and very thin wings (Fig. 6. I, II). The wings are erect, not slightly, but distinctly so that the thallus is concave above in a transverse section. Longitudinally, however, it presents a different appearance. The plant grows upwards from a thick base, but after some time it again grows downwards and bends its thick apex into the soil at the end of the vegetative season (Fig. 6, I). A median longitudinal section of an unbranched thallus or a lobe is concave below owing to the peculiar habit of the plant. At the end of the vegetative season the apex is thick but it is not covered with scales which are found on the sides only and has very few rhizoids. The apical part rests in this condition during the dry season and grows upwards again next year. This goes on year after year.

The dorsal surface is densely papillated, as pointed out by Falconer, but not without pores as he says. The "papillæ" in reality are minute, slightly raised pores, which cannot be seen by an ordinary lens. Each pore is surrounded by four or five cells with very thick radial walls (Fig. 6, VI). The pores lead down to a single layer of slit-like spaces which can hardly be called chambers as they are so narrow (Fig. 6, IV, V). They are hardly wider than the slits of a typical *Riccia* thallus. The number of cells surrounding these spaces as seen in a horizontal section is variable. The spaces are directed forwards obliquely. The ventral surface is also greenish or hyaline and is covered with numerous large white scattered scales; these have an entire margin Fig. 6, VII) and a

¹ One more species of Athalamia has been recently discovered by the writer in another part of the Himalayas, viz., Pangie It diccious and has wider air chambers.

triangular or lanceolate outline. There is no trace of an appendage in any part of the scale, though occasionally a cell may project slightly outwards from the margin. The scales bend over the growing point in the apical depression and form a conspicuous white tuft. The rhizoids are of both kinds, smooth and tuberculate.

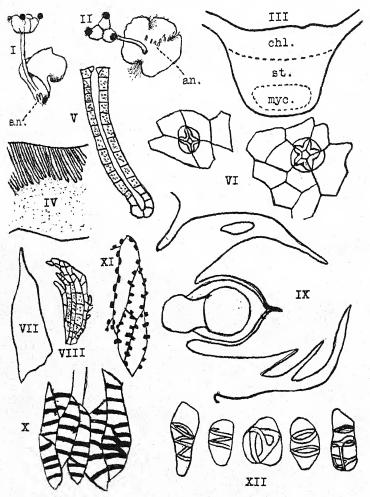


Fig. 6. Athalamia pinguis. I, side view of plant, \times 2; II, surface view, \times 2 (an., papillæ of antheridia). III, transverse section of old thallus, \times 12 (chl., chlorophyllous layer; st., starchy region; myc., mycorrhizal region). IV, longitudinal section of thallus, \times 12. V, part of IV, \times 50. VI, two stomata as seen from above, \times 200. VII, young ventral scale, \times 12. VIII scale from a young female receptacle, \times 50. IX, horizontal section of involucre with young sporogonium, \times 50. X, part of capsule wall as seen from the inside, \times 200. XI, same as seen from the outside, \times 200. XII, elater-like cells from apex of capsule, \times 200.

The plant possesses a definite mycorrhizal region in the centre of the midrib in the older parts (Fig. 6, III). Below the upper green layer the cells of the compact portion except those of the mycorrhizal region are full of starch grains. Here the cells are filled with fungal hyphæ and with minute granules which stain brown with iodine, but there is no starch. It may be mentioned that fungal hyphæ were also seen in the cells of the midrib of both the species of Plagiochasma previously described, Aitchisoniella, and Reboulia hemispherica. The cells containing hyphæ in these cases also have no starch but contain granules staining brown with iodine. In these forms, however, the mycorrhizal region is not sharply separated from the surrounding tissue, the cells containing the hyphæ being more or less scattered in the midrib. In all cases, including Athalamia, hyphæ were found also in the smooth rhizoids, hence it appears that they penetrate into the thallus by means of these rhizoids.

The plant is usually monocious. Falconer could not make out any antheridia, probably because they had discharged their contents and the papillæ had withered, and also because sometimes antheridia may not occur on a thallus or a lobe bearing archegonia. The antheridia are generally found behind the female receptacle, sometimes in front of it, and occasionally on distinct lobes which have no female receptacle, in two zigzag rows. The chambers in which the antheridia are situated open by large hyaline papillæ (Fig. 6, I, II). The papillæ project from the surface of the thallus and are not arranged on any raised tissue. In this respect the plant resembles Sauteria more than Clevea. The female receptacle arises on the dorsal surface in the middle line. Sometimes two receptacles may be formed one after the other. The young receptacle is surrounded by many small scales, which differ from the ventral scales of the thallus: their margins are not entire but have numerous cells projecting outwards and forwards, they are smaller, and many of their cells possess chloroplasts which are absent from the ventral scales (Fig. 6, VIII). These scales are carried at the top of the stalk of the receptacle later on, and are found at the base of the ripe receptacle. They are, however, closely attached to the receptacle and are in no way conspicuous. There are no scales at the base of the stalk.

The receptacle produces many archegonia, up to eight, each contained in a bilabiate involucre with thin valves and open down

¹ NEW PHYTOLOGIST, Vol. 13, 1914, pp. 318-332.

to the stalk. The latter is thick and cylindrical less than 10 mm. in length. It is circular or more or less triangular in transverse section and more or less sulcate. Sometimes the ripe receptacle is quite sessile.

There is no disc, or tissue proper, of the receptacle, or it may be represented by a minute round knob where the involucres meet. but it has no stomata. The involucres have chambers in their tissue which, however, open irregularly only inwards by large holes (Fig. IX), as is the case in Sauteria.1 The involucres are directed upwards. Not more than five ripe sporogonia were found in any receptacle, though eight involucres were counted in many. In some cases only a single ripe sporogonium was present. The sporogonium has a well developed foot, and the capsule, which is fully exserted and directed upwards, has a long seta. The latter may be up to 1.5 mm. in length. The calvptra is thin and is ruptured into two pieces by the growing sporogonium. The capsule wall is formed by a single layer of cells which are strengthened by simple U-shaped bands on the inner and radial walls. The outer walls are quite thin (Fig. 6, X, XI). The spores are brown, tetrahedral and covered with numerous obtuse papillæ on the surface. They appear reticulate in a surface view but the papillæ project from the margin and give the latter a toothed appearance. They are 65 to 70μ in diameter. The elaters are trispiral, sometimes branched, and 140 to 200µ long. At the apex of the capsule are some short elater-like cells attached to the inner surface and hanging into the cavity. They are spirally or annularly thickened, and the bands sometimes anastomose irregularly (Fig. 6, XII). A few similar elater-like cells, but only annularly thickened, are also attached to the base of the capsule projecting upward into the cavity. The capsule dehisces by four or five valves to the base. The valves are ultimately reflected backwards so as to touch the seta.

The plant resembles Sauteria in the structure of the male and female receptacles, but is nearer Clevea in the dorsal position of the female receptacle and the structure of the capsule.

GOLLANIELLA PUSILLA ST. (Fig. 7).

Stephani described a plant from Mussoorie under the above name in 1905 (Hedwigia, Bd. 44, p. 74). The writer has collected specimens from that place which answer to Stephani's description in most respects, but differ in a few points. Moreover, as the writer was able to clear various details in the structure of the plant

¹ Leitgeb, "Untersuchungen über die Lebermoose," Heft 6, Taf. 2, Fig. 11.

which Stephani was unable to make out owing to the nature of the material he used, the following description was drawn up.

The plants were found growing in patches on several eastern slopes which were more or less protected, on bare rocks or on crumbling hard soil closely attached to the substratum. The thallus (Fig. 7, I) grows from a narrow thick base and is a thin delicate structure forking once or twice. The apex at the end of the season becomes slightly thickened and is slightly bent downwards. persists in this condition throughout the dry season and continues its growth next year, and this fact explains the thick base of the plants. The latter are small, delicate and thin, though the midrib is comparatively thick. They may be up to 15 mm. long and 1.5 mm. broad. There is often a small median groove on the dorsal surface near the anterior end. The dorsal part of the thallus has a single layer of rather small air chambers which, however, are not so narrow as in Athalamia (Fig. 7, IV). The stomata are regularly scattered on the dorsal surface and each is bounded by two rings of cells with five or six cells in each ring. The walls of the cells are perfectly thin, like those of the cells of the epidermis (Fig. 7, V). The stomata are only slightly raised and very inconspicuous. The ventral surface is greenish, sometimes reddish, and has rhizoids of both kinds and many small scattered scales (Fig. 7, II). The latter are delicate, hyaline or reddish, lanceolate-acuminate structures from whose margin numerous cells project outwards. The cells of the scales contain chloroplasts. The apex is formed by a short filament of four or five cells, and shorter filaments may project from the margins also (Fig. 7, VI). The thallus gives off ventral adventitious shoots occasionally.

The sex organs are arranged in the same way as in Athalamia pinguis. The plant is usually monœcious, but occasionally a plant may have only antheridia or archegonia. The usual position of the antheridia is behind the female receptacle (Fig. 7, I). Occasionally they are formed in front of the female receptacle, especially if the thallus forks after producing the latter. They are arranged in two zigzag rows, and the hyaline papillæ of the antheridial chambers project slightly upwards. Their number is always small, half-adozen or so.

The female receptacle arises on the dorsal surface along the middle line and is an extremely minute protuberance when the archegonia are formed. The young receptacle is surrounded and covered by small simple linear scales whose cells contain chloroplasts

(Fig. 7, VII). Two or three receptacles may be formed in succession. Often only a single archegonium is produced, occasionally two, so that in the mature state the receptacle has a single involucre (Fig. 7, III) or sometimes two involucres each containing a single sporogonium (Fig. 7, I). Later on the receptacle is raised on a stalk, but

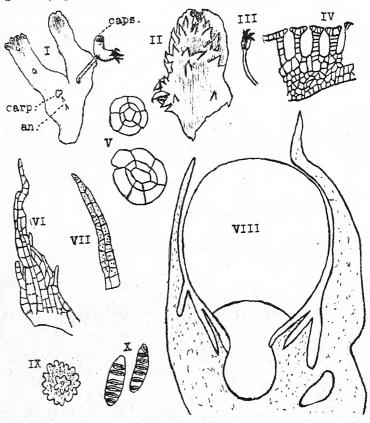


Fig. 7. Gollaniella pusilla. I, plant from above, \times 4; an., antheridial papillæ; caps., capsule; carp,, base of a broken carpocephalum. II, thallus from below, \times 12. III, carpocephalum with one involucre, \times 3. IV, part of longitudinal section of thallus, \times 50. V, two stomata, \times 200. VI, scale from ventral surface, chloroplasts not shown, \times 50. VII, scale from young female receptacle, \times 50. VIII, horizontal section of involucre with a nearly ripe sporogonium, \times 50. IX, spore, \times 200. X, elater-like cells from apex of capsule, \times 200.

only if the archegonium is fertilised. The scales also are carried upwards and are found at the base of the ripe receptacle. There is no proper tissue of the receptacle at all. The bilabiate involucres are directed upwards and their walls have spaces which open by large holes on the inner surface, exactly like those of *Athalamia* (Fig. 7, VIII). The peduncle is about 5 or 6 mm. long, cylindrical

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and sulcate. The calyptra is thin and ruptured into several pieces. The ripe sporogonium has a well developed foot, and the capsule is fully exserted and directed upwards. The seta is 1 to 1.5 mm. long. The ripe capsule wall, consisting of a single layer of cells, has well developed thick annular and spiral bands—not semi-annular bands as described by Stephani-on the cell-walls. The cells at the apex have thicker and deeper-coloured spiral bands and form a sort of operculum. Attached to the inner surface of this operculum there are a few small elater-like cells with annular thickening bands only, and they hang into the cavity of the capsule. A few similar cells are also attached to the base of the capsule and project upwards into the cavity (Fig. 7, X). The spores are brown, 45 to 50μ in diameter, with numerous high papillæ on the surface (Fig. 7, IX). The elaters are bispiral, brown, 140 to 180μ in length. The capsule opens by four or five valves down to the base. The valves bend backwards when the capsule is dry.

The plant is clearly closely related to Athalamia, and hence to Clevea, as pointed out by Stephani. The difference is chiefly in the structure of the stoma.\(^1\) The capsule is very much alike in both. It may also be pointed out that Athalamia, Gollaniella, and Clevea have a striking resemblance to the Targionia group in the structure of the capsule wall and the presence of the fixed elater-like cells at the apex and the base. Hence Leitgeb's group Astropora is more nearly related to the group\(^2\) formed by Exormotheca, Aitchisoniella and Targionia than his group Operculata. As regards the structure of the thallus Aitchisoniella and Gollaniella form a sort of connecting link between the two groups. It is known that fixed elater-like cells at the base and apex of the capsule also occur in Fegatella conica and Pressia commutata (Cavers, "Inter-relationships of the Bryophyta," Reprint, p. 48; Annals of Botany, Vol. 18, 1904, p. 87).

I have great pleasure in expressing my best thanks to Dr. Cavers, to whom I am greatly indebted in several ways in the publication of these papers. Not only have his published works been of assistance to me, but he has also taken great pains in supplying references to the literature of the subject, to which his own valuable papers have contributed so much, in correcting the proofs

¹ Since the above was written the writer has come across some plants of Gollaniella pusilla in another part of the Himalayas. They are much more robust, and the stomata on them have distinctly thickened radial walls, though not so much as in Athalamia. If some forms of this species have semi-annular bands on the cells of the capsule wall, as described by Stephani, the separation of this genus from Athalamia cannot be natural.

² See phylogenetical table given in the beginning of these notes (New Phytologist, Vol. 13, 1914, p. 209).

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and in arranging the figures properly. As stated in a footnote (New Phytologist, Vol. 13, p. 217), it was at his suggestion that I gave a variety name to the form of Targionia hypophylla met with at Mussoorie.

ADDITIONS AND CORRECTIONS.

Note on Aitchisoniella. In the first paper of this series the existence of the pores of the antheridial chambers in this genus was said to be doubtful (New Phytologist, Vol. 13, p. 222). Fresh and younger plants have shown since then that such pores do exist though they are very slightly raised and are very inconspicuous. In this respect, therefore, Aitchisoniella does not differ from the other Marchantiales.

Note on Nomenclature. In the first paper of this series the writer gave a list of the thallose liverworts found at Mussoorie (New Phytologist, Vol. 13, p. 208). Some of these plants whose identification seemed to be doubtful were sent to Professor Stephani for determination. He very kindly sent the names of all that could be identified, but they arrived too late to be published before now. His determinations are as follows:—(1) Riccia discolor is R. himalayensis; (13) Grimaldia californica is G. indica St.; (18) and (19) are Marchantia palmata Nees and M. nepalensis L. et L.; (20) Aneura pinguis is A. mussuriensis St.; (25) is Notothylas Levieri Schiffner.

Riccia himalayensis, I think, need not be separated from R. discolor. This species is met with in many parts of the Himalayas and even lower down on the plains where R. discolor has been found by several people at various times. The differences in the two forms are probably due to local conditions.

I sent some specimens of Cyathodium tuberosum to Professor Goebel some time ago, and he informed me that my specimens were identical with C. penicillatum St. Having myself examined a bit of the latter kindly sent by him, I find that this is indeed the case. I have not, however, come across any published description of this plant.

Errata. New Phytologist, Vol. 13, 1914, p. 214, line 4 from top: for "Griffithia" read "Aitchisoniella"; p. 216, line 2 from bottom: for "there" read "here."

CONCRESCENT AND SOLITARY FOLIAGE LEAVES IN PINUS.

By L. A. Boodle, F.L.S., Jodrell Laboratory, Royal Gardens, Kew.

[WITH FOUR FIGURES IN THE TEXT.]

A BNORMAL specimens showing concrescence of the two needle leaves on a spur-shoot were discovered by Strasburger¹ in two species of Pinus (P. Pumilio and P. sylvestris), and were described by him in connection with his interpretation of the morphology of the double needles of Sciadopitys verticillata.

A similar abnormality has been found on a tree of Austrian Pine² growing in the Royal Botanic Gardens, Kew. Most of the foliage of this tree is normal, but pairs of concrescent leaves are produced every year in fair numbers.

The nature of the fusion between the two leaves is illustrated by the transverse section shown diagrammatically in Fig. 1. This section was cut near the base of the double leaf, viz. at a height of 4 mm. above the basal sheath of scales. The structure is identical with that of two normal leaves of the same species, except for the differences immediately connected with the fusion, the mesophyll of the two leaves being continuous at m, and the epidermis and hypoderm (ep. hy.) respectively being continuous on either side of m. The fusion described above may be continued from the base to near the apex of the two leaves, but never quite to the apex, two free leaf-apices being always present. At a short distance below the point at which these tips become free, the tissue connecting the two leaves shows a decrease in breadth, which continues until, in the last transverse section showing concrescence, the leaves are only united by one or two epidermal cells at the extreme margin.

Measurements of twenty-five specimens of double leaves gave 9.5 mm. as the average length of the free portion, and 89.0 mm. for the concrescent portion. In one case the free part was only 1 mm/long, and in another case it was 47 mm. long, these being the two extremes observed.

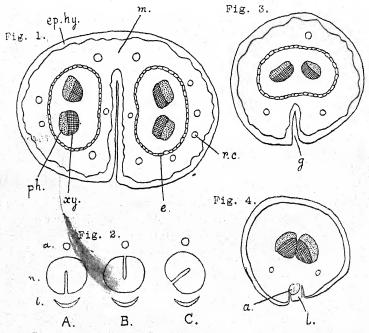
The examination of a considerable number of twigs on the tree on which the abnormality was found, gave the result that one or more double needles are present among the tuft of needles at the end of nearly every twig. The leaves on the spur-shoots on six

¹ Strasburger, "Die Coniferen und Gnetaceen," 1872, p. 387.

Pinus Laricio Poir. var. nigricans Parl. (=P. Laricio var. austriaca Endl.)

twigs were counted, and the numbers of leaves were as follows. There were 602 normal pairs of leaves, 20 double leaves and 6 solitary leaves, i.e., 6 leaves each borne singly on a spur-shoot.²

One of the features of this case of concrescence is its simplicity. It is clear that only the two normal leaves are represented, and there appears to be no necessity to assume that any of the tissue in the region of concrescence is other than leaf-tissue. At any rate in a case like the present one, in which the apical growth of the shoot becomes arrested, it may be held that reduction in the bulk of the apical cone might involve the suppression of some



Figs. 1-4. Austrian Pine (Pinus Laricio Poir., var. nigricans Parl.).

Fig. 1. Transverse section of double needle: ep. hy., epidermis and hypoderm; m., mesophyll; r.c., resin-canal; e., endodermis; xy., xylem; ph., phloem. x about 30.

Fig. 2. Diagrams illustrating variable orientation of the double needles: a., twig or parent axis; l., scale-leaf borne by the twig; n., double needle borne by the spur-shoot in the axil of l. A, adaxial fusion; B, abaxial fusion; C, oblique orientation.

Fig. 3. Transverse section of a solitary leaf, showing the groove, g. x about 30.

Fig. 4. Transverse section through the base of the same leaf, showing two protuberances, apparently the apex of the spur-shoot, a., and the rudiment of the second leaf, $l \times a$ bout 30.

¹ Normal except that in a few cases one leaf was a good deal shorter than the other.

^{*} These solitary leaves will be described later.

tissue which normally separates the bases of the two leaf rudiments. The latter would then be continuous, and a concresent structure would result, which may be regarded as entirely foliar in origin, unless visible indications to the contrary can be adduced. The fusion always extends less than half way across the transverse section of the double leaf, and, when the bases of some specimens were examined, a small papilla, apparently representing the apex of the short shoot, was found between the partially fused leaves.

The orientation of the double leaves is not constant. Cases were found in which the leaves were fused by their adaxial margins, *i.e.* the margins directed towards the twig, and away from the scaleleaf in the axil of which the spur-shoot with its two foliage-leaves is borne (Fig. 2, A). Other cases show fusion of the abaxial margins (Fig. 2, B), and obliquely placed-concrescent leaves also occur (Fig. 2, C).

It appears quite probable that the double needles of Sciadopitys verticillata may be morphologically similar to those of the Austrian Pine described above; that is they may represent two foliage-leaves fused by their margins. On this assumption the two leaves in Sciadopitys would be united by their adaxial margins, as shown by the orientation of the vascular bundles. Hence the double leaves of Sciadopitys would agree, as regards orientation, only with such double leaves of the Austrian Pine as correspond to diagram A in Fig. 2. Neither a spur-shoot nor a separate apex representing it can be recognised in Sciadopitys, so the double needle of this plant may be regarded as the result of fusion of two foliage-leaves belonging to a spur-shoot, which has been suppressed. This view was held by H. von Mohl.¹

Other theories must be recognised as tenable, e,g. that of Strasburger,² who regarded the double needle as the result of the concrescence of two leaves with one another and with the apex of the spur-shoot. Goebel³ interprets the double needle as a leaf-like twig or phylloclade, bearing on its primordium the tips of the two needles as small points. A teratological specimen, which was regarded by Bower⁴ as giving support to this view, should be referred to here. The specimen owed its origin to the proliferation of a cone of Sciadopitys, and resembled a double needle at its base, but was

¹ H. von Mohl, Bot. Zeit., Vol. 29 (1871), p. 21.

² Strasburger, loc. cit., p. 388.

³ Goebel, "Organography of plants," Eng. ed., Part 2 (1905), p. 445.

⁴ Bower, Gard. Chron., N. S., Vol. 21 (1884), p. 346; see, for figure, p. 282 of the same volume.

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forked into two branches above. One of these bore higher up an apparently simple needle and also a scale-leaf with a small twig in its axil.

Of the six solitary leaves of the Austrian Pine mentioned above three were of quite normal form, and a withered stump of the second leaf was found on each of the three spur-shoots.

The three other solitary leaves were abnormal, being roughly cylindrical in form. In two of these a groove was present on one side of the leaf, and was continued upwards for some distance from the base. It is seen at g in Fig. 3. On following the groove downwards in a series of transverse sections, it was found to contain, right at the base of the leaf, two papillæ, one of which (a in Fig. 4) appears to represent the apex of the spur-shoot, and the other (l in Fig. 4) to be the arrested rudiment of the second leaf. In the third specimen the leaf showed no groove except at the extreme base, and in this case only one papilla was found.

In Pinus monophylla Torr. the spur-shoots mostly bear each a single needle, but two are occasionally present. When the leaf is solitary, it is roughly cylindrical, but when two leaves are present, each is nearly semicircular in transverse section. Masters² found by studying early stages that two leaf-rudiments are always produced, but that one of them generally becomes arrested at an early stage. Hence the solitary leaves of Pinus monophylla are strictly comparable with those found on the Austrian Pine. Arrest of one leaf on a spur-shoot, which is a rare occurrence in the latter species, has become general in the former.

It is not unlikely that both double and also solitary needles may occasionally occur on other species of *Pinus*^s besides those mentioned here. As the abnormal needles are by no means conspicuous among the normal foliage, they are liable to escape notice.

A double needle of *Pinus*, like the examples described above, may be regarded as being produced by partial fusion of two normal leaves, though other views are not refuted. The normal needle of *Sciadopitys* may be somewhat similarly interpreted, but as showing more complete fusion of the two leaves, with suppression of the spur-shoot and its scale-leaves. Solitary needles, occasionally found in some species of *Pinus*, originate in the same way as the typical leaves of *Pinus monophylla*.

¹ Solitary leaves similar to these appear to have been seen by Strasburger (loc. cit., p. 389) in *Pinus Pumilio*.

² Masters, "Pinus monophylla." Ann. Bot., Vol. 2 (1888), p. 124.

 $^{^3}$ A few cylindrical solitary leaves have peen found on a tree of Pinus muricata D. Don.

AN ABNORMAL SHOOT OF PINUS THUNBERGII PARL.

By W. C. Worsdell, F.L.S.,

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[WITH FIVE FIGURES IN THE TEXT.]

A N apical piece of shoot of *Pinus Thunbergii* Parl. shewing unusual features was forwarded to the Director of Kew Gardens by Sir E. G. Loder, of Leonardslee, Horsham. The Director placed it at my disposal for description. The terminal portion of the shoot, which exhibited the abnormality, was about 8 inches in length, and bore four or five buds at the apex.

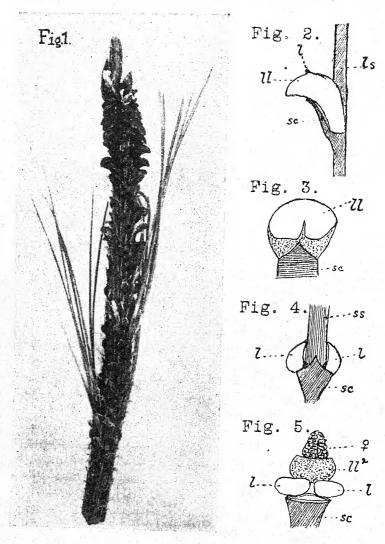
Eight or nine of the scale-leaves in the lower half of the length of shoot bore ordinary 2-needled spur-shoots in their axils. The majority of the remaining scale-leaves subtended quite a different kind of axillary shoot, and in this consists the abnormality to be described. I have seen a considerable number of shoots and cones in the Abietineæ which diverge, in one way or another, from the usual conformation, but never before have I come across such a condition as that which is about to be described.

The most frequent form which the abnormal axillary structure assumes is that of a swollen fleshy foliar organ arching outwards over or against the subtending scale-leaf. Such structures are aggregated in great numbers towards the apex of the shoot below the group of buds. Frequently these bright-green swollen leaves bear a distinct outgrowth on their adaxial surface, sometimes a pair of such outgrowths; and these clearly represent one or two further leaves situated higher up on the axillary shoot, which have become fused with the lowermost recurved one.

Another form which the axillary shoot assumes is that of a pair of transversely-placed fleshy leaves, each about half the size of the single recurved leaf above-mentioned, or smaller, enclosing between them one or two extra smaller pairs of fleshy foliar organs. All these leaves, from those of the first pair upwards, may be, owing to the very contracted space in which they arise, considerably displaced from the normal position, and here and there irregular fusions may occur, as also correlative modifications in development.

In several cases the spur-shoots begin with the same transverselyplaced pair of fleshy leaves, as in the cases of the axillary shoots just cited, being immediately followed by the usual scale-leaves of the spur-shoot.

There is yet a third kind of axillary shoot to be noted; this occurs to the number of three or four in the lower part of the piece of shoot. It is inaugurated by the usual pair of green fleshy leaves;



Figs. 1-5. Pinus Thunbergii.

Fig. 1. Photograph of terminal portion of a shoot, showing the recurved fleshy leaves in the upper part. Fig. 2. Recurved fleshy leaf in axil of scale-leaf (lateral view). Fig. 3. Anterior view of same. Fig. 4. Pair of transversely-placed fleshy leaves at base of spur-shoot (anterior view). Fig. 5. Two pairs of fleshy leaves at base of rudimentary female cone. Lettering:—ls, long shoot; st, scale leaf; ll², cupule; ll, fleshy leaves fused; l, fleshy leaf of second pair; ss, spur-shoot; ?, female cone. Fig. 1 about one-half nat. size. Figs. 2—5 semi-diagrammatic, x about 2.

this is succeeded by a brown cupule-like structure, apparently formed by a second pair of transversely-placed leaves, in which case the intervening median pair would be suppressed. Within the cupule is what appears to be a diminutive withered, black female cone, for it consists of a short axis bearing a number of scattered double foliar appendages, each of which may be compared with the double leaf formed by the "bract" and ovuliferous scale of the ordinary female cone, but no sign of ovules could be discovered.

Reverting now to the afore-mentioned recurved fleshy leaves which occur singly (or with extra leaves of the axillary shoot on their adaxial side), in greatest number in the upper part of the shoot, it was determined that this recurved leaf is formed through the fusion, by their adaxial margins, of the two transversely-placed leaves which occur in so many of the axillary shoots, with which is incorporated, at least in the basal region, one or two of the succeeding pair of leaves which may or may not undergo (this could scarcely be determined) some revolution in orientation. This mode of origin of the outward-arching scale could only be accurately determined by its anatomical investigation, for although the slightly bilobed character of many of these scales seems to imply their compound nature, the exact mode of union of the component leaves could only be demonstrated when it was seen that the vascular bundles, forming a row of strands across the leaf, were orientated in such a way that their xylem was directed outwards (downwards). In the basal region of the leaf, besides this row of strands, were two others on the dorsal (adaxial) side which were irregularly orientated, as if the two foliar organs to which they belonged (represented by two conspicuous ridges), were undergoing a certain amount of revolution or torsion preparatory to their eventual more complete fusion, at a higher level, with the main leaf.

Particular attention must now be directed to the comparison which may be made between these curious recurved leaves of the axillary shoot on the one hand and the ordinary "needles" of Sciadopitys on the other. The "needle" of this latter plant is the result of fusion by their adaxial margins of the first two (transverselyplaced) leaves of the shoot axillary to a scale-leaf. The recurved axillary leaves of Pinus Thunbergii (albeit abnormal), afforded, therefore, another case of vegetative leaves being formed in this way, the case of Sciadopitys being the only normal one known.

¹ One of the interesting cases in which the origin and nature of an organ can only be finally settled by the anatomical method of investigation.

26 An Abnormal Shoot of Pinus Thunbergii Parl.

Strasburger¹ described and figured a case of fusion by their adaxial margins of the needles of *Pinus Pumilio* Hænke; Mr. L. A. Boodle informs me that he has seen similar fusion of needles in *P. sylvestris* L. and *P. muricata* D. Don; the present writer has seen the specimens which he collected. In these cases the fusion, however, was sometimes by the adaxial and sometimes by the abaxial margins.

These cases of *Pinus* are not wholly comparable with those of the recurved fleshy leaves of *P. Thunbergii* Parl. and with the "double needle" of *Sciadopitys*; for the needles of *Pinus* are not the first-formed leaves of the axillary shoot, being preceded by a number of scale-leaves; they may be also variously orientated, a fact which will account for the variation in the mode of marginal fusion.

The best comparison of all may be made between our recurved leaf and the ovuliferous scale of the Abietineæ, for, according to the most popular view of the latter, the mode of origin of the two is precisely identical. In both cases, also, one or two leaves situated at a higher level on the axillary shoot have become incorporated into the double foliar organ; the apophysis or umbo on the adaxial side of the ovuliferous scale finds its replica in the curious outgrowth (representing the tip of one of the next pair of leaves) occurring in the upper part of the adaxial surface of the fleshy recurved leaf.

With regard to the physiological meaning and cause of the abnormal condition of the piece of shoot, the equilibrium of the whole has evidently become upset, possibly by the presence of a fungus, which has been ascertained to be present. The axillary shoots have been stimulated to an exceptional degree and mode of development, but the reason for the particular forms which they have taken is obscure.

At any rate, the phenomenon of the recurved leaf and its mode of origin lends strong support to the prevailing view of the morphological nature both of the ovuliferous scale of Abietineæ and of the "needle" of *Sciadopitys*. For it indicates the existence of a tendency in the Coniferæ for the first two leaves of an axillary shoot to unite by their adaxial margins to form a single dominant axillary foliar organ.

The abnormal shoot under discussion affords, further, a powerful substantiation of the view that teratological phenomena are often of great value in throwing light on the nature and origin of otherwise obscure structures.

Strasburger, "Die Coniferen und Gnetaceen," 1872, p. 387.

² Mr. G. Massee investigated the shoot for this purpose.

STEPHEN HALES, A REPLY TO CRITICISM.

By Francis Darwin.

[N the New Phytologist, Vol. XIII, p. 194, Professor Harvey Gibson criticises some remarks of mine in The Makers of British My statement "Hales, of course, knew nothing of Botanv. stomata" is careless, but if its context is taken into account it can hardly be considered inaccurate. After a comma at stomata the sentence continues: "but it is surprising to find Sachs in 1865 discussing the problem of transpiration with hardly a reference to the effect of stomatal closure." The words quoted by Harvey Gibson are also immediately preceded by a discussion on Hales' observation of nocturnal diminution in transpiration, concluding with the words: "This difference may be accounted for by the closure of the stomata at night." So that the words criticised are guarded on both sides by expressions which might have shown my critic what was meant, viz., that Hales knew nothing of stomatal closure.

I am also called to task for saying that Hales "does not in any way distinguish between respiration and assimilation." My critic quotes from Hales:—"we may therefore reasonably conclude that one great use of leaves is what has long been suspected by many viz., to perform in some measure the same office for the support of vegetable life that the lungs of animals do for the support of animal life; plants very probablydrawing through their leaves some part of their nourishment from the air." This sentence seems to me to justify my contention that Hales did not distinguish the two processes in question. But here again Harvey Gibson considers I am wrong, and proceeds: "Crude as was the knowledge of animal physiology in the time of Hales it can scarcely be believed that Hales conceived the lungs to be nutritive organs, and the sentence quoted therefore seems rather to indicate that he regarded the leaves as serving both as a respiratory and as a nutritive apparatus."

The foundation of Hales' views on the nutrition of plants was the sentence he quotes from Newton, "Dense bodies by fermentation rarify into several sorts of Air; and this Air by fermentation, and sometimes without it, returns into dense bodies." ²

¹ I am glad to find that I am in agreement with the late J. R. Green (A History of Botany from the Earliest Times, &c., p. 203) who remarks that, in the passage quoted, Hales "seems to confuse the two processes of respiration and nutrition, but neither of these had taken shape in scientific thought."

² Vegetable Staticks, 1727, p. 165.

On this basis Hales formed his theory of vegetable nutrition, concluding (p. 211) "that particles of air in a fixt state" adhere to and are "wrought into the substance" of plants.¹

It is quite clear therefore that for Hales the entry of air into leaves was a process of nutrition.

To discover whether Hales distinguished between assimilation and respiration, we must know something of the views current in his day. The history of our knowledge on respiration is given in Michael Foster's most interesting Lectures on the History of Physiology (1901). It is there shown how large a share Englishmen had in the unravelling of the mystery of respiration, and it can hardly be doubted that Hales knew the writings of Lower and Hooke on this subject; he certainly knew Mayow's. Lower had shown that in respiration air is absorbed by the blood. And he concluded that it is as much needed for animal life as for the burning of a candle—"in fact where a fire burns readily, there can we easily breathe." ²

Mayow's contribution (published in 1668 when he was 25 years of age) was to show that only a part of the inspired air was essential for breathing, and by this part, "though he called it by a different name, he meant what we now call oxygen." He studied the action of oxygen, or as he called it the "igneo-aerial particles" of air, by experiments on combustion. His later experiments show that he considered the burning of a candle and the respiration of an animal to be comparable. But he did not for this reason exclude the conception of assimilation. Indeed the contrary seems more probable, for he says that a flame enclosed in a flask "goes out not because it is suffocated by its own smoke, as some have thought, but because it is deprived of its aerial sustenance or food (pabulum)."

In describing the case of "a small animal and a lighted candle... shut up in the same vessel," he remarks (p.192) that the animal lives after the candle has gone out. "So soon" he says "as the igneoaerial particles begin to reach the flame scantily and slowly, it is soon extinguished. For animals, on the other hand, a lesser store of the aereal food 5 is sufficient, and one supplied at intervals, so that

¹ He is here especially referring to the nutrition of apples, but on the same page he expresses his general belief that "air makes a very considerable part of the substance of Vegetables, as well as of Animals."

² Quoted by Foster, p. 184.

Foster, loc. cit., p. 186.
 Foster, loc. cit., p. 188.

Italics mine.

the animal can be sustained by the aereal particles remaining after the candle has gone out."

It is interesting to find Mayow saying (p. 195) that "not even plants can grow in earth the access of air to which is shut off.... It is clear that even the very plants seem to have some need of breathing, some need of drawing air into themselves."

It is certain that Hales was acquainted with Mayow's experiments since he repeated them as described in Vegetable Staticks (1727), p. 244. After speaking of animal respiration he goes on: "And nature seems to make use of the like artifice in vegetables, where we find that air is freely drawn in; not only with the principal fund of nourishment at the root but also through several parts of the body of the vegetable above ground," and so into the minute vessels "where being intimately united with the sulphureous, saline and other particles, it forms the nutritive ductile matter out of which all the parts of vegetables do grow."

It would be unreasonable to ask for clearer evidence of my assertion that Hales did not distinguish between respiration and assimilation.

Poster points out how Mayow "saw that igneo-aerial particles, i.e., atoms of oxygen" were "essential for all the chemical changes on which life depends." He knew that food was also necessary for these vital processes. Whether he made any sharp line of distinction between the two, I do not know, but in any case Hales did not.

¹ Italics mine.

² Wiesner has pointed out (Jan Ingen-Housz, sein Leben, &c., 1905) that in 1838 Meyen and Dutrochet were still striving to make clear to the world the difference between assimilation and respiration in plants.

REVIEW.

FLOWERING PLANTS OF THE RIVIERA: A DESCRIPTIVE ACCOUNT OF 1800 OF THE MORE INTERESTING SPECIES.

By H. Stuart Thompson, F.L.S. With an Introduction on Riviera Vegetation, by A. G. Tansley, M.A. London (Longmans, Green & Co.), 1914, pp. xxviii and 249, 32 plates (24 coloured, 8 photographic).

Price 10/6 net.

THIS book fills a much felt gap in the literature available to the tourist in a region where even the least observant cannot fail to be struck with the great variety and brilliant colouration of the wild flowers.

Few persons could have been more competent to deal with the task of providing a simple and compact account of this very large flora than Mr. Stuart Thompson, who has had long personal acquaintance with the region and whose previous volumes on Alpine Plants and Subalpine Plants have ably demonstrated his powers of

writing a popular yet scientific flora.

The flora is arranged on the system of Bentham and Hooker, which only departs in minor points from that generally used in French floras. The actual descriptive part is preceded by a compact and useful synopsis of the families in which the essential distinguishing characters are given in a few lines. Each family also is in its turn provided with a synoptic table of the tribes and genera, and though no keys to the species are given the descriptions are short and clear and in most cases should present no difficulty. The terms used are those in general use in all English floras, while for the beginner a full and clear glossary of terms is given. Further help is furnished in identification by the coloured plates of a large number of species. These plates are from drawings by Mr. Clarence Bicknell and form a valuable addition to the work. They should add greatly to its popularity with the general public. The figures on the plates in one or two cases lose something of their artistic merit from being a little too close to the edge of the paper. Also the plates in many cases are inconveniently far from the descriptions of the plants illustrated.

The book, as its title indicates, does not profess to be an exhaustive flora, but perhaps, from the point of view of the botanist, one may be forgiven for feeling a slight regret that, while the descriptions given are so excellent, a rather closer approach to completeness has not been attained. This feeling of incompleteness is especially noticeable in the case of some of the larger genera and families, under which many species are often simply mentioned by

name. However, it must be admitted that these cases nearly all refer to groups which the non-professional botanist would be apt to avoid. The treatment awarded to the Gramineæ is scarcely on a level with that given to other families, which seems unfortunate in a region in which, if grasses are not dominant, a very large number of species occur, many of very striking appearance. Thus it is a little trying to be faced with a sentence such as "The following species occur, some of them being very pretty grasses" followed by a list of sixteen names but no distinguishing characters (p. 239).

The author has wisely avoided the thorny subject of strict nomenclatorial rules. He tells us in the preface that the names used are not in all cases governed by exact priority, but generally accepted names are retained. The synonyms that are given are few, in fact they are only used in cases of plants to which several different names have been applied in standard works. One is glad to see that no attempt has been made to manufacture so-called English

names for species generally unknown in this country.

The book is provided with two introductions. That by Mr. A. G. Tansley is on Riviera Vegetation and gives in a very short space a clear picture of some of the more striking features of the distribution of plant associations in the region. The relations of soils and of shelter from the hot drying effects of the Mediterranean sun are well brought out. The account is tantalizingly short and leaves the reader with a great longing to hear more. This account is illustrated by reproductions of several excellent photographs taken by Mr. Thompson. These show clearly some of the more characteristic features of the vegetation and several of the more noticeable plants.

The other introduction is by Mr. Thompson on methods of collecting and preserving plants and is a valuable and clear account not only useful to the beginner or amateur but also to the

professional botanist who is amassing a herbarium.

The volume is printed on thin but sufficiently opaque paper and though a little large for the average pocket is light and easily carried. It should certainly be in the hands of every visitor to this most favoured part of Europe.

R.S.A.

REVIEW.

NOTES ON THE BLUE-GREEN ALGÆ, WITH A KEY TO THE SPECIES OF OSCILLATORIA AND PHORMIDIUM.

By HAROLD WAGER, F.R.S.

London (A. Brown & Sons), 1914, 48 pp., 2/6 net.

THE key, which is the most important part of this little book. is reprinted from The Naturalist for 1913. The idea is to provide a purely artificial key, in a readily accessible form, to the commoner species of these two genera, without relying primarily on the characters of the sheath. "It is based mainly on the structure of the trichome as given in Gomont's Monographie des Oscillariées," and sheath characters are used only when there can be no doubt of their visibility. The diagnoses are not intended to be critical, and references are given to Gomont's monograph, to Tilden's "Minnesota Algæ," and to Forti in de Toni's "Sylloge Algarum" for full diagnoses and figures. The key should certainly facilitate the identification of these rather difficult genera and is useful in bringing together the references to the monographs. There is a short introduction dealing with the general structure of the members of the group and a key to the orders and families, from which, however. the Glaucocystidea are omitted. A glossary is added: it seems slightly unnecessary, however, to explain such terms as chromatin, nucleus and epiphyte in a book of this type. The book is well printed, excellent use being made of different types in the arrangement of the key. There are two slight misprints, "Tricohphoreæ" appearing for "Trichophoreæ," and "Chamæsiphoniaceæ" for "Chamæsiphonaceæ."

S.R.P.



NEW PHYTOLOGIST.

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NEW MARINE FUNGI ON PELVETIA.

By Geo. K. SUTHERLAND.

[WITH FOUR FIGURES IN THE TEXT].

THE small number of known marine fungi stands in striking contrast to the long list of land species, especially when the extent and the variety of possible algal hosts are considered. A natural inference that such forms would be mainly simple Phycomycetes, like the Chytridineæ occurring on fresh-water algæ, has led to a search for these, but, owing to their minute size and to the difficulty of observing them under anything like natural conditions, the investigations have proved distinctly disappointing, both in point of species recorded and the knowledge of their life-histories. Little systematic attention has been paid to other groups, with the result that, while one or two species were known as early as the middle of last century, the additions have been few and accidental. In a survey of marine Pyrenomycetes, published in 1907, Cotton gives a list of nine known species, one of which he describes for the first time. Of these, only two are recorded for this country. Several new and interesting fungi have been collected by the writer in a careful examination of algæ at various points along the coast of Britain. In the present paper it is proposed to deal only with some of those occurring on Pelvetia.

The dark olive-green, lichen-like zone of *Pelvetia canaliculata* is one of the most characteristic and distinctive features of our seaboard, forming a narrow belt near the upper reaches of the tidal, and along those outer rocks which project into comparatively shallow water at high tide. The densely crowded much-branched thalli, attached to the rock surface by more or less discoid holdfasts, mark the upper limit of the Fucaceæ. There they lead a dual existence, at one time swaying freely with the advancing and retreating waters, at another exposed to the full influence of sun

and air, without any means of renewing their water supply. They are submerged at most only for a few hours each day, while during neap tides the water may not reach them for two, three, or even four days. This holds only during fine weather; when the sea is rough the plants become drenched with spray or foam, even when the tides are neap. The result is that *Pelvetia* normally spends the greater part, and periodically the whole, of each day under conditions very similar to those enjoyed by many lichens to which its thallus bears a strong external resemblance.

The abundance and wide distribution of *Pelvetia*, coupled with its amphibious habit, tended to mark it out as a possible and likely fungus host, an initial hypothesis which has been fully verified by a systematic examination of this alga throughout the past year. It has been found to possess a rich fungus flora, hitherto undescribed. Some are saprophytic, some parasitic. One symbiotic species is of special interest as its occurrence throws a new light on *Pelvetia*, opening the question whether it should be regarded as a lichen rather than an alga.

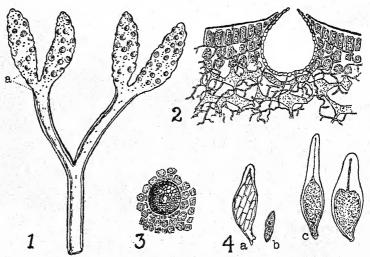
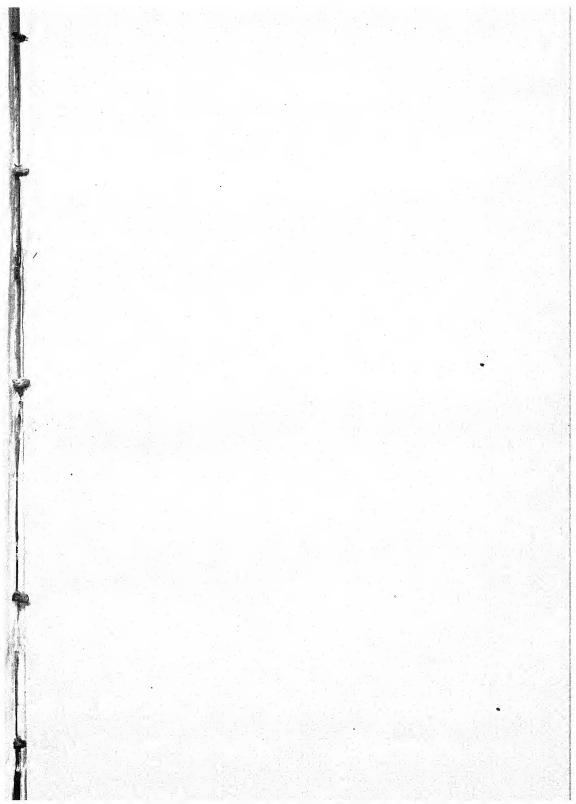
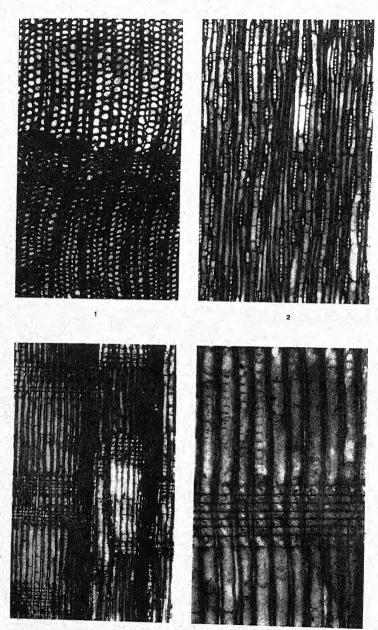


Fig. 1. Mycosphærella pelvetiæ. 1, Pelvetia thallus and receptacles showing perithecia (a); 2, section showing perithecium and intercellular hyphæ magnified out of proportion so as to render more visible; 3, surface view of perithecium; 4, asci (a, c) and ascopore (b).

MYCOSPHÆRELLA PELVETIÆ NOV. SP. (Fig. 1, 1-4).

Mycelium hyaline, septate, very slender, diffused and entirely intercellular. Perithecia minute, $65-85\mu$, spherical, with small conical tip, densely aggregated on receptacle. Perithecial wall





London Stereoscopic Co., imp.

HOLDEN-A JURASSIC WOOD.

thin and membranous except at exposed tip. Asci cylindrical and curved, or tapering, thickened apex almost pierced by narrow canal, $45-55\mu \times 15-20\mu$. Ascospores biseriate or bunched, fusiform, $19-25\mu \times 4\cdot5-5\cdot5\mu$, hyaline, uniseptate, with slight constriction, cells biguttulate when mature.

Hab. Symbiotic with Pelvetia.

The very slender septate mycelium of this fungus permeates every portion of the thallus from holdfast to receptacle, running along the surface of the algal cells, with whose outer walls it is in very close contact. In colour it resembles the latter, and this, added to the extreme tenuity of the hyphæ, may explain why it has been constantly overlooked. The threads, so fine as rarely to exceed 1-1.25 μ in diameter, are difficult to detect without the aid of stains; iodine and fuchsin make them readily visible.

The mycelium is entirely intercellular, never breaking through the soft slimy walls unless the cells have been attacked and partially broken down by parasitic fungi or bacteria beforehand. When the material is in this condition the course of the symbiotic mycelium cannot be traced with the same certainty. In the healthy thallus there is no such difficulty. The large intercellular spaces of the medullary tissue and cortex, kept moist continually by the swollen mucilaginous walls, form an ideal home for the hyphæ whose branch tips penetrate even between the cells of the rind or limiting layer. The hyphæ branch freely and are extremely numerous, forming a loose net-like web surrounding the cells. Altogether there is an immense length of fungus to unit-volume of the tissue, but with it all not the slightest trace of injury to the host has been noted in the hundreds of sections examined.

The fungus grows along with the thallus and thus penetrates into the young receptacles, where it commences to fruit just as the reproductive bodies are being formed in the conceptacles. Minute perithecia are produced immediately under the rind, through which the tips burst and barely protrude when mature as in Fig. 1, 2 and 3. While the immersed portion of the perithecial wall remains thin and membranous, the small projecting tip becomes carbonaceous, and thus readily visible against the olive-green receptacles, so that at this stage the latter become marked by numerous small black specks as in Fig. 1, 1 (a). The perithecia are practically confined to the receptacles; a few scattered ones may appear on the thallus immediately below, but they rarely, if ever, occur on the main vegetative body of the host.

These small spherical or pyriform fruiting-bodies contain a small number of asci which are of various ages and formed successively. The diversity in shape of mature asci, found even in the same perithecium, prevents their form being taken as a distinctive feature, notwithstanding the fact that it is often so used by the systematist. While many are broadly oblong and curved as in Fig. 1, 4 a, others have long, tapering, much thickened apices almost completely pierced by narrow canals with slightly swollen lips as in Fig. 1, 4 c. Prequently the thickened apical portion forms half of the total length of the ascus when mature. Paraphyses are wanting.

The ascospores, eight in each ascus, are fusiform, hyaline, uniseptate and slightly constricted. Each cell becomes biguttulate when ready to be dispersed (Fig. 1, 4b).

Not only is the mycelium of this fungus slimmer than that of Mycosphærella ascophylli, first noted by Church in 1893, and described and named by Cotton in 1907; perithecia, asci, and ascospores also differ. These points alone are sufficient to justify its being regarded as a separate and distinct species.

The ascospores are set free from the perithecia about the same time as the oospheres are being liberated. They become entangled in the mucilaginous inner persistent oogonial wall surrounding the latter. There they germinate and their germ-tubes gain entrance to the developing oospore either directly or sometimes a short mycelium is formed which penetrates slightly later. Thus the fungus finds its way into the intercellular spaces at a very early stage in the development of the young alga. Infection is rendered doubly sure by a vegetative process. Mixed with the paraphyses in the conceptacles are loosely coiled, much branched hyphæ. These frequently become entangled in the mucilaginous coating enveloping the oospheres and are torn off as the latter are ejected. This mycelium is also capable of growing and gaining entrance to the developing oospore, when it again lodges between the young cells

Curiously no perithecia have been observed in the thallus of *Pelvetia canaliculata* var, *libera* (Oliver) although abundant mycelium is present. This form, found only at Blakeney, reproduces by vegetative means alone. The fungus has adopted a similar habit being carried into the new shoots before they separate from the parent plant. The absence of perithecia, correlated with the absence of reproductive bodies in the algal host, shows how close the union between the two has become.



Very early in the season smaller and differently shaped perithecia were observed. These appeared to be pycnidia, but unfortunately no pycnidiospores were found in the material collected.

The mycelium of this fungus seems to occur in every thallus. Thousands of plants have been collected and sectioned from stations representative of the North and South, of the East and West coasts of Britain. All showed the fungus; in fact no plant, examined by the writer hitherto, has failed to show it in profusion. In addition, herbarium material at Kew has been gone over with the same result. These specimens were representative of Europe generally, and of collections made from the beginning of last century to the present day. This would seem to confirm the writer's view that this union of alga and fungus is general. It is quite possible, however, that oospores may germinate and plants reach maturity without infection. It will be interesting to determine whether this is so, and also to find out the distribution of such plants if any occur.

The wide, and it may be universal, occurrence of the mycelium along with *Pelvetia* at once raises the question of the relationship of the two. Experiments have been initiated with a view to determine, if possible, the part played by both in this symbiotic union. It may quite well be that the presence of the fungus has something to do with the plant's ability to withstand exposure for so long after submersion. Observations in the laboratory have shown that the loss of water from the thallus is very slight. But here again it is too early to make definite assertions as the experiments and observations are still incomplete.

STIGMATEA PELVETIÆ NOV. SP. (Fig. 2, 1-6).

Perithecia arranged in almost concentric rings on blackened patch, sunk in tissue, forming hemispherical protuberances with flat or occasionally rounded bases, remaining covered by blackened tissue except at point broken by irregular ostiole, large, $160-200\mu$ in diameter. Peridium only distinctly formed near tip. Asci cylindrical, long with slightly thickened apex, $100-120\mu \times 12-14\mu$, 8-spored. Paraphyses present, branched and unbranched, septate. Ascospores egg-shaped, $22-25\mu \times 9-12\mu$, hyaline, uniseptate, with distinct constriction. Pycnidia smaller, pyriform, with thick black walls, $70-85\mu$, at first sunk, but becoming superficial; pycnidiospores $3 \times 1.5\mu$.

Hab. Parasitic on thallus of Pelvetia in Scotland.

This fungus is parasitic, attacking the thallus and doing such damage as frequently to sever branches from the basal portions.

The disease is marked externally by the blackened circular patches shown in Fig. 2, 1, 2. Usually the margins of these become white owing to the disintegration of, and consequent chemical changes in, the rind of the host. The hyaline, slender, septate mycelium is entirely local, and is easily distinguished from that of Mycosphærella, with which it is intermingled, by its greater thickness and irregularity, as well as by its habit. Its average diameter is $2-2\cdot 5\mu$ but frequently it reaches as much as 5μ at points where the branching is extensive. The spaces between cells become packed with the hyphæ which penetrate the mucilaginous walls and become closely coiled round the living contents into which haustoria are sent as in Fig. 2, 4. At other times the tips of branches penetrate directly and act as absorptive organs. In this respect this plant differs markedly from the symbiotic fungus already described.

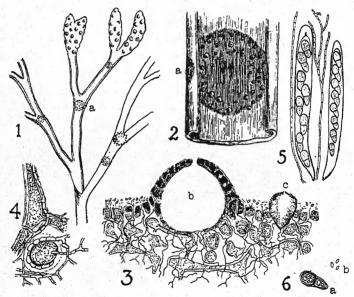


Fig. 2. Stigmatea pelvetiæ. 1, thallus with diseased spots (a); 2, diseased patch enlarged; 3, section showing perithecium (b) and pycnidium (c); 4, mycelium with haustoria; 5, asci and paraphyses; 6, ascospore (a), pycnidiospores (b).

Growth is rapid and shortly after infection fruiting bodies appear on the blackened patches in the form of small pycnidia corresponding to the genus *Phyllosticta*. At first these are immersed but they become superficial by the disintegration of the surrounding tissue. The walls are thick and carbonaceous. Minute elliptical conidia are ejected from the small ostiole. The rapid infection,

following the first appearance of the disease, is doubtless due to the quick dispersal and immediate germination of these small bodies.

The ascigerous fruits appear slightly later on the same patches. They originate in masses of mycelium in the cortex, which increase and give rise to asci before distinct perithecial walls are formed. The place of the latter is taken largely by the superincumbent layers of the host which become blackened to form a kind of false clypeus. This becomes raised to form a hemispherical dome pierced later by the irregular ostiole. A thin perithecial wall is formed under this but it does not extend along the flattened or occasionally curved base, bounded only by the mass of hyphæ from which the reproductive bodies spring. The poor development of the peridium may be accounted for by the protection given by the blackened overlying tissue, represented in Fig. 2, 3. As this becomes thinner the membranous wall is formed.

This method of perithecium formation has been noted in other fungi examined by the writer in alga. When placed in the mucilaginous bodies of the latter there is less need for protective walls.

The perithecia are large and readily visible to the naked eye. They contain numerous long cylindrical asci with very slightly thickened tips and mixed with longer septate branched and unbranched paraphyses as in Fig. 2, 5. The hyaline spores are uniseptate with a distinct constriction marking off the upper broader cell from the lower narrower one. When mature they contain several oil globules.

In the broken-down tissue on the surface of the blackened patch numerous hyaline elliptical conidia are found. As the tips of hyphæ penetrate into this layer it may be that these are cut off from them. They are seen in Fig. 2, 3.

This species is placed in the genus Stigmatea with some reservation. The spore characters, asci, paraphyses and some other features combine to ally it with this genus. It is, however, a moot question whether the origin of the perithecium and its distinctive character do not justify its being placed in a separate and new genus. This can be settled definitely only when the other algal fungi are examined and the whole matter of perithecium formation studied with regard to the new conditions involved in this type of host.

PHARCIDIA PELVETIÆ NOV. SP. (Fig. 3, 1-3).

Mycelium thick, brown, and parasitic, frequently forming a superficial web in addition. Perithecia minute, $45-55\mu$, spherical

and with projecting ostiole, at first sunk, finally superficial with brown leathery walls. Asci few, cylindrical with short thickened rounded apices, $30{\text -}35\mu \times 10{\text -}14\mu$, 8-spored. Paraphyses absent. Spores hyaline, two-celled becoming four-celled, surrounded by thin mucilaginous sheath, on the rupture of which the spore breaks at the weak middle into two portions, $12{\text -}15\mu \times 3{\text -}4{\text -}5\mu$.

Hab. Parasitic on Pelvetia in Britain.

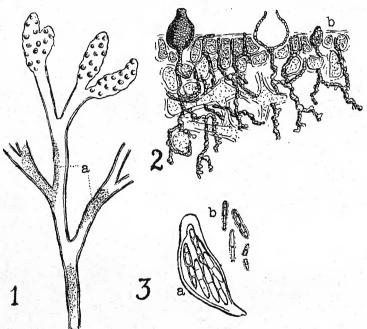


Fig. 3. Pharcidia felvetiæ. 1, thallus with perithecia on diseased patches (a); 2, section showing perithecia and dark-coloured parasitic mycelium; 3, ascus (a) and ascospores (b).

This fungus is likewise parasitic, but is easily distinguishable to the naked eye from Stigmatea by the irregular outline of the blackened areas and the immense number of minute perithecia represented in Fig. 3, 1. Its stout, brown mycelium consists of thick-walled irregular cells with an average diameter of $3-4\mu$, but frequently of 5μ or even more. It forms close coils around the host cells into which haustoria are sent.

Densely crowded hyphæ riddle the cortical layers and send branches along the surface forming a loose network in the brokendown rind. The rapid extension of diseased patches makes this parasite a powerful factor in preparing the thallus for the subsequent action of saprophytic fungi and bacteria. Immense numbers of small perithecia are produced shortly after infection. They become superficial and consequently have well developed thick leathery walls. The ascospores likewise are protected by a thin mucilaginous envelope.

PLEOSPORA PELVETIÆ NOV. SP. (Fig. 4, 1-4).

Mycelium thick, brown with irregular cells. Perithecia at first sunk, becoming superficial, large, black, leathery with short conical opening, $150-200\mu$ in diameter. Asci cylindrical or with free end slightly tapering, thin walled, $110-125\mu \times 25-30\mu$, 8-spored. Spores biseriate, elliptic-oblong, yellowish brown, generally seven cross septa and numerous vertical ones, slight constriction, $30-35\mu \times 12\mu$.

Conidial form believed to be *Macrosporium pelvetiæ*. Conidiophores branched or unbranched, 3μ , brownish. Conidia clavate, with 5-6 transverse and 1-3 vertical septa, $35-45\mu \times 11-12\mu$.

Hab. At first parasitic on Pelvetia, then saprophytic.

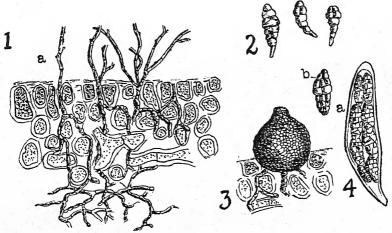


Fig. 4. Pleospora pelvetiæ (1, 2) and Macrosporium pelvetiæ (3, 4). 1, section of thallus showing mycelium and conidiophores of Macrosporium; 2, conidia of same; 3, perithecium of Pleospora; 4, ascus (a) and ascospore (b) of same.

This fungus produces very much the same effect upon plants attacked as does *Botrytis*. The thalli become withered and tend to break down into a brownish slimy mass. The thick brownish yellow mycelium penetrates and destroys the tissue; the whole medullary portion becomes a mass of parasitic hyphæ as in Fig. 4, 1. The cortical layers are also riddled and outside arise erect unbranched or slightly branched conidiophores (a) on which are borne the clavate muriform conidia shown in Fig. 4, 2. These vary considerably in shape, but usually show 5-6 transverse and one, two, or three vertical

septa. This undoubtedly parasitic stage would correspond to Macrosporium pelvetiæ nov. sp. Later the ascigerous fruits of Pleospora appear on the same spots and on identical mycelium. This would seem to make the Imperfect fungus the conidial stage of the Pyrenomycete. But culture experiments are necessary to make this point certain although this type of conidium is common to other species of Pleospora.

The perithecia are large and at first sunk in the thallus, but finally become superficial. Paraphyses are present in the immature fruits, but later they break down and deliquesce.

In conclusion I wish to express my thanks and indebtedness to Mr. A. D. Cotton, who noted *Mycosphærella* previously, and kindly handed over to me his material collected at Blakeney and Clare Island, and also to Mr. L. A. Boodle, by whose courtesy this work was carried out in the Jodrell Laboratory.

University College, Southampton, December, 1914.

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VEGETATIVE PRODUCTION OF FLATTENED PROTONEMA IN TETRAPHIS PELLUCIDA.

By William J. Hodgetts.
[With One Figure in the Text.]

1.-INTRODUCTION.

In the great majority of mosses the protonema, or early phase of the gametophyte, is filamentous and monosiphonous, consisting of a single branching row of cells from some of which there arise buds which develop into leafy moss-plants—and this whether it proceeds from the germinating spore and thus forms part of the normal life-cycle of the moss-plant, or whether it arises by outgrowth of certain cells of the moss-plant or of the sporogonium itself (in the last case forming an example of apospory) and thus forms a deviation which lengthens or (by apospory) shortens the life-cycle, serving for vegetative propagation.

There are certain exceptions to this rule, in which the whole or part of the protonema is ribbon-like or cylindrical. The remarkable protonema of Schistostega, which sends up from its creeping filamentous portion erect filaments whence arise repeatedly branched chains of lens-like cells all lying in the same horizontal plane, is strictly monosiphonous although the branching chains of cells in the aerial assimilating portion form virtually a plate. True thalloid or flattened protonemata occur in the monogeneric orders Sphagnales (Sphagnum) and Andrewales (Andrewa), the Tetraphidales (with the two genera Tetraphis and Tetradontium), the Buxbaumiales (with the two genera Buxbaumia and Diphyscium), and the rare and isolated genus Œdipodium which is usually placed in or near the family Splachnaceæ though its affinities are obscure. It will be noted that with the exception of Edipodium, flattened protonemata are characteristic of four out of the five orders of mosses which are for other reasons regarded as being relatively primitive.1

In Sphagnum the germ-tube arising from the spore soon becomes a plate of cells which may reach a considerable size before producing, usually from a marginal cell near the base, the bud from which a new moss-plant develops. Müller² has made the interesting observation that numerous secondary protonemata, or innovation lobes, arise as outgrowths at various points from marginal cells of

See classification given by Cavers, "Inter-relationships of the Bryophyta," New Phytologist, Vol. 10, 1911, pp. 26-34.

² Müller, in Engler and Prantl, Teil 1, Abt. 3, p. 163, Fig. 82.

an old Sphagnum protonema which had not had its growth arrested by the production of leafy shoots. Oehlmann¹ has shown that Sphagnum has hitherto been incorrectly regarded as forming an exception to the general rule among Bryophytes that every living cell of the plant is capable under favourable conditions, naturally or in cultures, of producing protonema, for he found that protonema could be formed from isolated leaves and pieces of stem of Sphagnum and—a specially interesting point—that this protonema was of the same flattened type as that arising from the spore and had the same capacity for giving rise to secondary protonemata by proliferation.

In Andrewa the protonema is extremely polymorphic. Here the spore-contents divide before rupture of the coat so as to form a mass of tissue—a thing which very rarely occurs in mosses though found in a fair number of liverworts—and one or more of the cells of this mass then grow out to form either filaments or more often branching ribbon-like or cylindrical structures which bear flat leaf-like appendages, the "protonemal leaves." The cylindrical protonema may grow erect to form a "protonemal shoot" bearing "protonemal leaves." All these forms of protonema sooner or later bear the buds from which the normal moss-plants arise. It may be noted that the only form of vegetative reproduction known in Andrewa is by the breaking off of branches which give rise to new plants.

Our knowledge of the protonema in the other genera mentioned is mainly due to the work of Berggren,² who followed its development from the spore in *Tetraphis*, *Tetradontium* and *Diphyscium*, while recently Jongmans³ has described the germination of *Œdipodium*, and Müller⁴ and Correns⁵ have added new details regarding the protonema of *Tetraphis*. In *Buxbaumia*, as figured by Roth,⁶ the protonema is a round plate of cells from which filaments arise, hence the early stage appears to be much the same as in *Andrewa*,

¹ Oehlmann, "Vegetative Fortpflanzung der Sphagnaceen nebst ihrem Verhalten gegen Kalk." Inaug.-Diss., Freiburg, 1898. Warnstorf ("Sphagnales-Sphagnaceæ" in "Das Pflanzenreich," Heft 51, p. 27) says he has never observed such protonemata in nature and that the conditions under which Oehlmann obtained them are not likely to be of frequent natural occurrence.

² Berggren, "Studier öfver mossornas bygnad och ütveckling. ii. Tetraphideæ." Lunds Univ. Arsskr., 1879.

³ Jongmans, "Ueber Brutkörperbildende Laubmoose." Rec. Trav. Bot. Néerland., t. 3, 1907.

⁴ Müller, in Engler and Prantl, Teil 1, Abt. 3, p. 167.

⁵ Correns, "Untersuchungen über die Vermehrung der Laubmoose." Jena (Fischer), 1899.

⁶ Roth, "Die europäischen Laubmoose," Bd. 1, 1904, Taf. 1, Fig. 4.

though later it is of the normal monosiphonous thread type, the extremely reduced male plants and the leafy female plants arising as buds upon it in the usual way. In *Œdipodium* the germ-tube is a row of cells which is soon converted into a plate by flattening of the terminal portion, "protonemal leaves" of similar form arising from it as outgrowths of the basal cells of the plate itself or of the short monosiphonous portion below. In *Diphyscium* the protonema arises in the same way, but the protonemal leaves have a curious trumpet-like form.

We now come to Tetraphis and Tetradontium, in which the germ-tube gives rise, either immediately or after growing and branching for some time, to spatulate protonemal leaves which occur in tufts owing to new "leaves" arising by proliferation from the bases of the older ones. In Tetraphis, Correns has described as arising from the germinating spore erect protonemal shoots ("Protonemabäumchen") resembling those of Andrewa. bore, however, instead of protonemal leaves, circular discoid gemmæ like those found in the characteristic gemma-cups of Tetraphis. Correns also describes and figures abnormal gemmæ, found in the axils of the outermost leaves of a gemma-cup; these are elongated and spatulate structures, presenting almost every possible transition between the filamentous paraphyses which occur among the gemmæ and sexual organs on one hand, and the gemmæ themselves and the protonema-leaves on the other. He also cultivated cut pieces of stem on moist sand and found that these gave rise to new plants, either directly or after first giving rise to a protonema leaf; in both cases the new growths proceeded from the outer cells of the stem and most often sprang from near a leaf, several sometimes arising from one leaf-axil.

The interest of the observations to be recorded below lies in the discovery that in *Tetraphis* flattened or thalloid protonema, exactly like that arising from the spore, may arise from the stems of plants growing under natural conditions. What Correns observed in cultures has now been observed in nature, though the cases are perhaps somewhat analogous, since in the plants here described the apex had ceased to grow and had from some cause been injured so that it consisted of dead cells.

II.—OBSERVATIONS ON TETRAPHIS.

The following curious method of vegetative reproduction was found occurring in a mass of Tetraphis pellucida growing on a

dead tree-stump in a bog near Birmingham. Many of the plants, none of which possessed any capsules, had the usual terminal crown

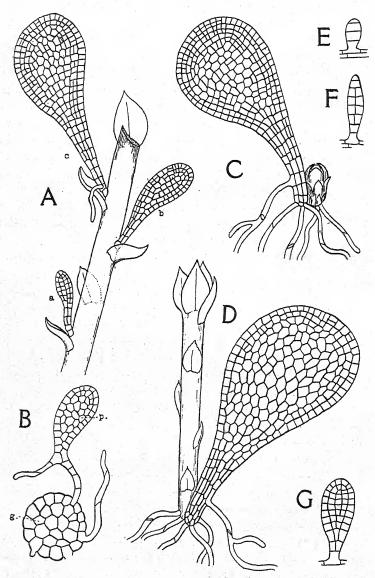


Fig. 1. Tetraphis pellucida. A, stem showing three thalloid protonema (a, b, c) growing from it, a little above the insertion of leaves. B, gemma (g) germinating and producing a young thalloid protonema (p). C, an independent (stem-formed) protonema which has produced numerous rhizoids and a basal bud. D, a young leafy stem which has been formed from a thalloid protonema. E, F, G, successive early stages in development of thalloid protonema from superficial cells of the stem. A \times 30; B \times 150; C to G \times 40.

of leaves containing gemmæ and were quite normal. In a considerable number, however, the apex of the stem had ceased to grow, and the stem ended abruptly in dead, brown cells. These plants had leaves of the ordinary Tetraphis type, which decreased in size downwards until at the base of the stem they were rudimentary and scale-like in character. But the most noticeable feature about these plants was the occurrence in the axils of many of the leaves (usually the upper leaves) of large thalloid outgrowths (Fig. 1, A).

These outgrowths are flat expansions, one cell thick, deep-green in colour, and of a spathulate form, with a narrow, tapering basal part, and a wide, rounded apex. They resemble in every respect the thalloid protonemata which are so characteristic of Tetraphis, and they are undoubtedly of this nature. As many as five of these outgrowths, of various ages, may occur on a single stem, but the average number is about three. In size they are anything up to 2 mm. long, and 1 mm. broad at their widest part, thus being considerably larger than the largest Tetraphis leaf. They arise in the first place as narrow tongue-like green outgrowths from the stem, immediately above the insertion of a leaf, but not quite in its axil. Fig. 1, A. shows three of these thalloid protonemata (the lowest one, a, being the youngest) on a leafy stem. The early stages in their development are shown diagrammatically in Fig. 1, E to G. They arise by the outgrowth of a single superficial cell of the stem, and are thus always fixed to the stem by a single connecting cell. Their cells from the earliest beginning are packed with chloroplasts and also contain abundant starch.

It is well known that similar thalloid protonemata are developed from the gemmæ (as well as from the spores) of Tetraphis on germination. Fig. 1, B, shows a gemma (g) germinating and developing one of these expansions (p). In no case could the protonemata growing on the stem be seen to be in connection with any gemma or spore.

When these thalloid expansions (growing from the stem) have reached a fairly large size one or more filamentous, colourless or brownish, rhizoids grow out from their narrow basal part (Fig. 1, A, c). These rhizoids usually become closely appressed to the stem down which they grow. They are of the ordinary moss type, with oblique cross-walls. The extreme basal cells of the protonema, where it is joined to the stem, are brownish in colour, and by the disorganisation of these cells the mature protonema can be readily be detached from the stem. It leaves a distinct scar on the stem at the point where the single connecting cell was attached; these scars were frequently seen on old stems, just above the insertion of the leaves.

Any one of these thalloid protonemata can, of course, give rise to a leafy shoot on becoming detached from the parent stem. They attach themselves to the substratum by numerous brown rhizoids, which grow out from the narrow basal part. Secondary thalloid protonemata may arise as outgrowths from any part of the primary one; they usually arise, however, from the narrow basal end, growing out into the air as leafy expansions. We thus frequently find a tuft of green thalloid protonemata arising from a mass of brown rhizoids, which fix them to the soil.

In Fig. 1, c and D show how the leafy stem arises from the protonema. In c a young bud has arisen at the base of a thalloid protonema; in D the bud has become elongated into a leafy axis. Leafy stems (and even stems with the terminal gemmiferous cup) can very frequently be found to be connected with thalloid protonemata at their base. Dixon remarks that the "frondiform leaves" (i.e., thalloid protonemata or "protonemal leaves") of T. pellucida "disappear before the development of the stem"; but a careful examination of almost any tuft of this moss will show some quite mature stems connected at their base with one or more "frondiform leaves." They appear to nourish the young leafy axis, and may flourish for a considerable time after the stem has become well established. It is interesting to compare this with the other British species of Tetraphidaceæ, namely Tetradontium Brownianum. This moss is almost stemless, its vegetative part consisting merely of a tuft of narrowly clavate "frondiform leaves," which may be somewhat palmately branched at the apex, and amongst which the capsule is produced.

Thus, besides the formation of numerous gemmæ, by which the plant most frequently reproduces itself, *T. pellucida* has another, apparently uncommon, method of vegetative reproduction in the formation of leafy protonemata from the stem. It should be noticed, however, that plants which resort to this method of reproduction have been precluded from forming gemmæ by the apex of their stem having been killed. Thalloid protonemata were never seen in the axils of the leaves of plants which had a terminal gemmiferous cup, nor of plants the stems of which had a living apex.

Although in Fig. 1 A, the oldest thalloid protonema is drawn nearest the stem-apex, and the youngest nearest the base of the

¹ Dixon, "Students' Handbook of British Mosses," 2nd Ed., p. 31.

stem, this order was not invariable; in fact the succession was frequently acropetal, and in other cases there was no definite succession at all.

III.—CONCLUSION.

Apart from Sphagnum and Tetraphis, none of the mosses which have flattened protonema appear to have been recorded as producing protonema vegetatively, but since the production of protonema from various parts of the leafy gametophyte is so common among mosses it appears likely that these forms with flattened protonema arising from the spore will be found on further investigation to be capable under natural or induced conditions of producing vegetative protonema, and it will be interesting to know whether the protonema thus produced is flattened like that arising from the germinating spore. In this connexion it is interesting to note that among the Hepaticæ the formation of the new plant from a germinating gemma takes place in the same way as in the germinating spore of the same species; in most cases the germinating gemma or spore gives rise to a germ-tube at the end of which the young shoot is developed, but in those forms which have discoid gemmæ (Aneura, Radula, the Lejeuneaceæ) the spore gives rise to a similar discoid protonema from the margin of which the shoot arises exactly as in the case of the gemma.1

The observations here recorded would appear to support the view that in *Tetraphis*, as in Hepaticæ with discoid gemmæ and discoid protonema, the gemmæ may be regarded as homologous with protonema though different writers have interpreted the gemmæ of *Tetraphis* as modifications of antheridia, paraphyses, mucilage-hairs, etc. This is also apparently the first case on record of flattened protonema arising vegetatively from the gametophyte of a moss under natural conditions as distinguished from cultures.

I wish to express my thanks to Mr. W. B. Grove for his kind interest and advice in connexion with this paper, and to Dr. Cavers who helped by supplying references to the literature and suggesting the comparisons between *Tetraphis* and the other Bryophytes mentioned in the introductory and concluding portions.

See Cavers, "Asexual Reproduction and Regeneration in Hepaticæ." New Phytologist, Vol. 4, 1903.

THE AUSTRALIAN MEETING OF THE BRITISH ASSOCIATION.

I.—THE BOTANICAL EXCURSIONS.

By E. R. SAUNDERS.

THE difficulty which confronted botanists attending the meeting of the British Association in Australia was that of selecting from among the large number of interesting expeditions which had been organised for their benefit. In each of the five capitals the programme included several day or week-end excursions, in some cases covering a considerable mileage, which only the most generous provision of motor cars rendered it possible to carry out.

WESTERN AUSTRALIA:

PERTH AND THE NEIGHBOURHOOD. THE MARGARET RIVER.

ALBANY.

For those who were able to arrive in Western Australia by the middle of July there was opportunity to explore the country around Perth before the official opening of the Meeting. Expeditions to Mundaring Weir and to various points on the slopes of the Darling range gave one an introduction to a characteristic landscape of evergreen forest vegetation with Eucalyptus as the dominant element, while the longer excursion to Yallingup and the Margaret River caves, involving a drive of some 70 miles through the bush. gave a splendid opportunity of seeing a larger extent of this type of forest vegetation. The Eucalyptus forest makes a very distinct impression on the mind of one seeing it for the first time; the height of the trees, the grey-white colour of the stems of many species, and the general absence of branches of any size for a considerable height from the ground, for 100 feet perhaps, are very striking. Several species are common in the Perth neighbourhood. e.g., the Jarrah (E. marginata) world-famed for its valuable timber,1 the Red Gum (E. calophylla), the Tuart (E. gomphocephala) and the White Gum (E. redunca), while in the extreme south-west is to be met the Karri (E. diversicolor), one of the giant trees of Australia. said to attain a height sometimes of 300 feet or more. A noticeable feature here and there are the huge dense masses of Loranthus

The fact that Jarrah timber appears to be less resistant to the attacks of termite and teredo now than formerly raises an interesting question and one of great commercial importance. Experiments are now being made to test the possibility of increasing the resisting quality of the wood by chemical treatment.

hanging from the lofty branches of the Eucalyptus trees, the leafform of tree and "mistletoe" appearing sufficiently similar from the distance of the ground as to make it difficult to discern where host ends and parasite begins. Species of Wattle (Acacia) are also numerous in this region, belonging mostly to the section Phyllodineæ. Among other trees of interest may be mentioned the She Oak (Casuarina), the endemic conifer Actinostrobus pyramidalis and the so-called Christmas Tree, Tree Mistletoe or Cabbage Tree (Nuytsia floribunda), a terrestrial member of the Loranthaceæ, also endemic. An interesting "find" was a quantity of young Nuytsia seedlings, some 3 to 4 inches in length, but showing no sign of root parasitism at this stage. Though full early for the West Australian flowers quite a large number of specimens were obtained in bloom. Among some of the more interesting herbaceous types may be mentioned several terrestrial Orchids, Caladenia Menziesii, Diuris spp., Prasophyllum parvifolium, Pterostylis reflexa and P. vittata, Thelymitra variegata var. spiralis; the common Daviesia, the conspicuous red Kennedya prostrata and Templetonia retusa, the beautiful blue Hovea trispermum and H. chorizemifolia, Bossiaa biloba with vellow-brown flowers and reduced leaves notched at the apex, and Facksonia, another yellow-flowered genus mostly of rigid, leafless plants (all Papilionaceæ); several species of Drosera with pink white or red flowers, and varying in size from plants with minute rosettes and scapes to climbing types some feet in length. The delicate stems of these climbing forms may come in contact with the upright shoot of a neighbouring plant up which they twine loosely or to which they cling by their glandular leaves, and are thereby enabled to reach a height of 4 or 5 feet (D. macrantha); or, failing such a support, they may lie in loose tangles on the low growth about them. When the sunlight catches the red glands with their drops of transparent secretion the effect is of leaves strung with tiny garnets and diamonds. Of the almost exclusively Australian families Goodeniaceæ and Hæmodoraceæ several representatives were obtained, including the brilliant blue Leschenaultia biloba, also Dampiera, Goodenia and Scavola (Goodeniaceæ); Anigozanthos, Conostylis, Tribonanthes brachypetala and Blancoa canescens (Hæmodoraceæ). Anigozanthos, the so-called Kangaroo Paw, with its asymmetrical structure and arrangement and its vivid colouring presents a most curious and striking appearance. In the larger species (A. Manglesii) the flowering stems were sometimes 3 feet high; when seen in bright sunshine the flannel-like surface of the stem and flower-base shows the most brilliant red, sharply marked off from the upper green flower-tube which is laterally split, and with its perianth teeth and its projecting anthers gives the suggestion of toes and claws which has presumably earned for the plant its Many members of the families, Proteaceæ, colloquial name. Myrtaceæ and Epacridaceæ which furnish so large a proportion of the shrubby vegetation of this region were already showing flower, e.g., of the Proteaceæ the purely Western genera Adenanthos (A. barbigera), Dryandra (D. nivea), Stirlingia (Simsia) and Synaphea; Lambertia multiflora, also a Western type; species of Conospermum (Smoke Bush), their grey-white inflorescences covered with a thick cottony tomentum, and also the more widely distributed forms Isopogon (I. roseus), Grevillea (G. bipinnatifida, G. oxystigma, G. Wilsoni), Banksia and Hakea. The species H. trifurcata was frequently found with a broad normal leaf here and there among the rest of the needle-like foliage.1 The persistent hard woody shell-like fruits of the last-named genus were a characteristic feature almost everywhere, as were also the large woody fruit cones of the previous season on the Banksias. Where an area is seen covered with Banksias in flower the handsome symmetrical inflorescences produce a most decorative effect. Of the Myrtaceæ may be mentioned Melaleuca (a Paper Bark or Tea-tree), Leptospermum (another Teatree), Agonis flexuosa (the Peppermint), Calothamnus a beautiful West Australian genus of the "bottle-brush" type and the pretty shrub Hypocalymma robustum; mention must also be made of the very pretty pink-flowered shrub Chamælaucium uncinatum, the Geraldton Wax-flower, specimens of which were very kindly obtained for us by residents in Perth from friends living further north. Of Epacrids the West Australian forms Andersonia (A. latiflora) and Lysinema (locally known as curry and rice). Of Liliaceæ the shrubby Calectasia cyanea an Australian type with a pretty blue everlasting flower. Two other types, often associated and dominating certain areas, strike even the casual observer. (1) The socalled Grass-trees or Black-boys belonging to the Liliaceous genera Xanthorrhea and Kingia, both with a stout, black caudex attaining sometimes a height of 15 feet and often branching at the top into several short trunks, each surmounted by a dense crown of long narrow leaves, erect and spreading when young, becoming reflexed and matted around the trunk as they get old. In Xanthorrhea

¹ See R. Brown, Trans. Linn. Soc., X (1810), p. 183. This peculiarity is also mentioned by Bentham in his "Flora Australiensis," Vol. V (1870), p. 504.

Preissii the single inflorescence spike arising from the top of the trunk-branches may measure 6 feet. In the monotypic Kingia (K. australis) several inflorescences of drum-stick form arise from the leaf-crown. When the old leaves are shed the bases are left surrounding the trunk as a complete sheath, giving it somewhat the appearance of a Cycad stem. This sheath in course of time becomes detached and breaks away piece-meal, so that fragments of broken rings which are rich in resin litter the ground. (2) The Cycad Macrozamia Fraseri, many plants of which were bearing cones, as many as 3 or even 4 being sometimes found on one individual. The cones of the present season were not yet mature; those of the previous year were lying on the ground gradually rotting and shedding the scales. The seeds lying thickly around were germinating freely. The fresh seeds are held to be poisonous to both men and cattle, but are said to be eaten by the aboriginals after they have been kept or buried for one or two seasons. The soft easily detachable woolly felt covering the crown furnished the early settlers with an economical bed-stuffing. Ferns were noticeably absent, but Cheilanthes tenuifolia was found in some quantity.

I cannot conclude this brief sketch of our botanical excursions from Perth without reference to the kind help of Mr. W. B. Alexander who accompanied the party on more than one occasion, and who gave us the greatest assistance all through in planning the trips and in naming specimens.

Albany proved another botanist's paradise. The ramble over Mount Clarence conducted by Mr. B. C. Andrews, who had organised the expedition and who most kindly travelled with the party from Perth in order to act as guide, yielded a large number of interesting specimens. Other expeditions were made in order to enable the party to see growing in abundance three plants of special interest, viz.. the fragrant brown-flowered Boronia megastigma (Rutaceæ) which is sold in the streets of Melbourne as lavender in London; the purely West Australian pitcher plant Cephalotus follicularis (Cephalotaceæ); and the Lycopod which few botanists have seen growing and which is confined to Australia and New Zealand-Phylloglossum Drummondii. The strobili of Phylloglossum were readily seen in the short turf, but the small rosettes of pitchers of Cephalotus close down on the boggy ground, and covered over by the surrounding vegetation, were easily overlooked. Of the other plants obtained only some of the most striking can be mentioned here, viz., the handsome white-flowered shrub Anthocercis viscosa (endemic,

Solanaceæ); in the same kind of rocky habitat another shrub Olax phyllanthi (Olacaceæ); Actinotus (Xanthosia) rotundifolia, the Southern Cross, so-called presumably owing to the arrangement of the four or five secondary umbels of each inflorescence in the form of a cross (endemic, Umbelliferæ); Callistemon speciosus one of the "bottle-brushes" and two other Mrytaceous genera, mostly confined to West Australia-Verticordia the Heath-myrtle with flowers with pink feathery calyx and corolla, Beaufortia (B. decussata and B. sparsa) handsome shrubs with vivid red inflorescences, and Actinodium Cunninghami with heath-like leaves; a pretty pale-blue Andersonia, Cosmelia rubra confined to south-west Australia, a species of the white-flowered west Australian genus Sphenotoma, and Leucopogon verticillatus, another Epacrid characteristic of this region, the genus being distinguished by its bearded petals: pinkflowered Tremandreæ (Tetratheca and Tremandra) and Boronias (Rutaceæ), three almost purely west or south Australian genera; a Phebalium, another endemic member of the Rutaceæ; Stylidium scandens, one of the "Trigger" plants with tendril-like leaf-tips, belonging to the nearly endemic order Candolleaceæ; Patersonia, almost the only representative of the Iridaceæ in Australia; three West Australian Papilionaceæ-the holly-leaved Chorizema ilicifolium, the heath-like Phyllota barbata with its woolly flower buds, and a species of Brachysema, a genus in which the shortness of the posterior petal (standard) gives the flower a somewhat deformed appearance; various species of Thomasia quercifolia a genus of the Australian family Sterculiaceæ; Comesperma an Australian genus of Polygalaceæ; Leptomeria the Native Currant (Santalaceæ); species of Anarthria and other Restionaceæ showing a marked difference between the male and the female plants; Johnsonia (Liliaceæ) an Australian genus of rush-like plants; Dasypogon bromeliæfolius another endemic Liliaceous plant peculiar to the south-west coastal area; Corysanthes, Eriochilus and Cyrtostylis reniformis with its single radical leaf, all three small terrestrial Orchids belonging to the tribe Neottineæ, the two latter being endemic.

SOUTH AUSTRALIA:

ADELAIDE AND THE VICINITY. MOUNT LOFTY. THE MURRAY RIVER.

At Adelaide those joining the Botanical expeditions were greatly indebted to Professor Osborn who not only conducted the excursions during our visit, but who had given much time previously to the exploration of the ground to be traversed, and to the preparation of maps, so that the utmost could be made by visiting members of the time available. The expeditions included long drives in the Mount Lofty range and to the Murray River Flats at Mannum; also an excursion to neighbouring points on the coast (Grange, Henley Beach, Glenelg) which enabled us to see something of this strip of coastal vegetation. As a sketch of the vegetation around Adelaide by Professor Osborn has already appeared in this Journal it is unnecessary for me to repeat here details which may be found in Professor Osborn's interesting paper.1

Brief reference to one or two points of interest must suffice. Our first objective was some mud banks on which were growing the white mangrove Avicennia officinalis (Verbenaceæ) with its numerous aerial roots rising vertically from the mud for some distance around the trees. The viviparous habit was not observable as the trees were then only in the early fruiting stage. The later coast walk afforded an opportunity of exploring a stretch of sand dunes, the vegetation of which consisted largely of shrubs. Among other species may be mentioned Grevillea ilicifolia, Alixia buxifolia (Apocynaceæ), Lasiopetalum discolor (Sterculiaceæ), a species of Myoporum, Rhagodia Billardieri (Chenopodiaceæ), Adriana quadripartita (Euphorbiaceæ), and a shrubby Epacrid Styphelia Richii. Trailing across the sand were the long stems of the well-known Spinifex not to be confused with the plant locally known as Spinifex which is Triodia irritans. An interesting and to most of us a novel experience was afforded by coming upon a stretch of musical sand. course of the day some typical loose balls of Salsola Kali, the socalled Roly-poly, were met with. These balls may sometimes measure as much as 3 feet across.

On the Mount Lofty range we had an excellent opportunity of seeing the sharp contrast between the slate and limestone hill slopes on one side of a valley, covered with grass and scattered Eucalyptus trees, but without shrubby undergrowth; and on the opposite side quartzite slopes bare of grass and covered only with a scrub vegetation of various shrubs. In the shrubby undergrowth of the Eucalyptus forest on the summits several Epacrids not previously seen were obtained in flower including Styphelia (Acrotriche) fasciculiflora and S. Sonderi and the common Epacris impressa with its variable flower colour; the shrub Bursaria spinosa (Pittosporeæ); there were also to be seen the parasitic green-

¹ New Phytologist, Vol. 13, 1914, p. 109.

stemmed Cassytha (Lauraceæ) and the Native Cherry (Exocarpus, Santalaceæ) so well known as having its stone outside the flesh, while the gully bottoms furnished a hunting-ground for various Ferns. These valleys are being increasingly brought under cultivation for orchards and market gardens, with the result that certain species formerly plentiful have now become scarce such as Gleichenia circinata. In addition to Gleichenia, specimens were obtained of Asplenium labellifolium, Lomaria discolor and L. capense.

In the course of the drive to Mannum very varied country was traversed, the route passing through first woodland, then a savannah region and finally the Flats which are being gradually reclaimed for wheat growing. In the tree region Eucalyptus rostrata and E. leucoxylon are the dominant types. In the savannah country the rises are occupied by Casuarina while the lower ground is covered with grass or in places with a carpet of a small species of Erodium. In these latter spots the small bare interspaces between the plants were overspread with a tangle of last year's shed fruits. On the Plats, where the original vegetation is still left, occur dwarf Eucalyptus forming the typical "Mallee" scrub, together with the native pine Callitris. At the river itself Azolla, which farther east we frequently saw covering areas like Duckweed here in England, and the thickets of "Lignum" (Muchlenbeckia Cunninghami, Polygonaceæ) growing along the edge of the "billabong" were the chief plants of interest.

(With so full a programme I was unfortunately unable to find time to visit the Botanic Garden, and I am therefore unable to say anything about it).

VICTORIA:

Excursions from Melbourne. The Melbourne
Botanic Garden.

Of the several excursions arranged at Melbourne those to Emerald and Warburton were of especial interest to botanists. In the course of the rail journey to Emerald there was good opportunity of seeing the Tree-ferns Alsophila australis and Dicksonia antarctica in their native habitat, while in the fern gully explored by the party on reaching its destination a closer view was obtainable. The ground was in cultivation up to within a few yards of the gully bottom, but in this bottom strip many specimens were

growing, among a dense interlaced growth of trees and shrubs. the case of some tree-ferns which had died, the top of the old trunk had served as the nursery for seedlings of neighbouring trees. Many, for example, presented the curious appearance of seeming to pass up into the stout stem of an Acacia tree, the root of which had grown down in close contact with the support and widening laterally had come to envelope it more or less completely. Other plants found included Hedycarya Cunninghami and Pittosporum bicolor, both characteristic of fern-tree country, Billardiera scandens another member of the Pittosporeæ, Pomaderris apetala (Rhamnaceæ), and of lianes, which are not numerous in this State, Lyonsia straminea (Apocynaceæ). In the course of the drive back to the railway several species of Acacia were obtained including A. juniperina with phyllodes of prickly needle-like form, and A. melanoxylon which furnishes a beautiful wood much prized by the cabinet maker. Among many other plants may also be mentioned Astroloma (Acrotriche) serrulata and Sprengelia incarnata of Epacrids, Lomatia Fraseri and L. ilicifolia, east Australian representatives of the Proteaceæ, the shrub Bauera rubioides (Saxifragaceæ) an east Australian type, and species of tough-stemmed Pimelea (P. flava, P. axiflora).

Those present on the Warburton expedition had an opportunity of seeing the methods in operation for the felling, haulage and cutting-up of big timber, for Warburton is a centre of the sawmilling industry. It is in this district that the mountain ash Eucalyptus regnans, Australia's tallest tree, attains sometimes to a height of 300 feet or more, rivalling in this respect the redwood (Sequoia gigantea) of California.

In the country just outside Melbourne the Acacias were already in flower, making woods and river banks golden with the profusion of bloom which on Wattle Sunday custom has permitted to be cut so freely for decorations with this national flower, that some restriction has now been found necessary.

The Melbourne Botanic Garden is known the world over for the extent and beauty of the grounds. A reception held in the Gardens passed a most pleasant social afternoon, and the occasion was commemorated by the planting by the President of the Association (Professor Bateson) of a young plant of Cupressus macrocarpa. The operation of planting was no mere pretence, requiring later "touching-up"; the tree was "well and truly planted" there and then.

NEW SOUTH WALES:

THE BLUE MOUNTAINS AND BULLI PASS AND CATARACT DAM
EXPEDITIONS. THE SYDNEY BOTANIC GARDEN.

Both these excursions proved extremely pleasurable, and the scenic attractions were so great as inevitably to claim a large share of attention. One could not, however, but regret that the extent of ground to be covered in the drives by motor necessarily left little time for leisurely collecting. One's attention was called to a bewildering number of new forms which too often were passed rapidly by before one had time to appreciate them. The great variety of country passed through makes it additionally difficult in a short space to do more than mention a few of the most characteristic plants. Along the route from Mount Victoria to Jenolan Caves more specimens of the genus Persoonia (P. linearis, P. ferruginea) were noticed than had been met with previously. The two rolledleaf species of Banksia, B. ericifolia and B. spinulosa, were to be seen, also several Leptospermum spp. (L. flavescens, L. scoparium, L. attenuatum), the Black Wattle (Acacia penninervis), and among numerous Eucalyptus forms E. viminalis (Manna Gum), E. amygdalina (Messmate or Peppermint), and E. melliodora (Yellow Box). The "sucker" habit of the Eucalyptus was a striking feature at many points on the road. Large trees of the River Oak, Casuarina Cunninghamiana, were seen marking the course of a stream. Near Jenolan Senecio lautus and S. australis were obtained in flower, also the introduced S. macranthus. Of the endemic Leguminous genera Dillwynia and Pultenæa, D. ericifolia and P. scabra were obtained. Hymenanthera dentata, a shrubby member of the Violaceæ, was another new type. Among smaller plants the Australian Sedge (Caustis flexuosa), known locally as "Curly Wigs," attracted attention owing to the curious appearance produced by the numerous slender recurved and interlaced branches.

At the beautiful view-points, Govett's Leap and Echo Point, a stay of a few minutes was made, and at the latter spot a rapid descent some way down the gully and a somewhat slower ascent afforded some general impression of the vegetation in these mountain gullies, where there is abundant moisture and shelter. Here under the shade of the so-called Mountain Acacia (a pinnate-

¹ This term is used locally to indicate the adventitious shoots which bear leaves of the juvenile type, and not as with us, shoots thrown up from the roots.

leaved form) were large numbers of the now familiar tree-ferns, while smaller fern types and numerous mosses occupied the moist ground space.

The Bulli and Cataract Dam expedition, passing near enough to the shore of Botany Bay to give a glimpse of the monument commemorating Captain Cook's landing place, followed a coast road to Bulli, affording opportunity of seeing in sheltered dips typical "brush" flora composed of Malayan rather than Australian Here and there en route the landscape flamed with the brilliant flowers of the Coral tree (Erythrina, Leguminosæ) planted around homesteads or in orchards, the leafless branches one glory of scarlet clusters. The tree vegetation of the brush is very varied, and Eucalyptus, as a rule, forms no part of it. Tree-ferns, of course, are abundant. One characteristic brush type was found in flower, viz., the strongly scented Sassafras (Doryphora sassafras, Monimiaceæ), a tree with white down-turned flowers. Ceratopetalum gummiferum (Cunoniaceæ), the well-known Christmas bush which is much in request at Christmas time for decoration purposes, was also met with. A striking element of the vegetation in this coastal region is the well-known Cabbage Palm (Livistona australis). The introduced Lantana camara was seen in one or two places; where the brush is opened up this plant spreads so rapidly as to become a pest. Near Waterfall the Giant Lily, Doryanthes excelsa (Amaryllidaceæ), was conspicuous with its large radical tuft of sword-shaped leaves and its tall stem 10 to 15 feet high bearing a cluster of red flowers. To speed relentlessly on across a stretch of high level ground—a real paradise of flowers—was most tantalising, but botanists present by courtesy on an engineers' expedition must bow to time-table exigencies, and we could but glimpse the plants as we passed rapidly by them. Conspicuous among new types was the purple-flowered Mirbelia speciosa (Leguminosæ). At the Dam itself the pretty pink Boronia ledifolia (Rutaceæ) was abundant. It was too early to obtain the gorgeous Waratah (Telopea speciossisima, Proteaceæ) in flower, though the plant was seen both on this and the previous expedition.

A much longer time than most botanical members were able to compass could well have been spent in the beautiful Botanic Garden at Sydney. Many, however, managed to explore it in some degree and to enjoy the kind hospitality of Mr. J. H. Maiden, the Director. All botanists indeed visiting Sydney owed to Mr. Maiden a deep debt of gratitude for the immense amount of time and labour which he had expended on their behalf before their arrival, and to his kind help all through their stay. Nor can I conclude without mentioning our great indebtedness to Mr. R. H. Cambage, Chief Mining Surveyor of the State, for his tireless energy and assistance on the expeditions. I gladly take this opportunity of expressing my personal thanks to them both.

QUEENSLAND:

BRISBANE. A QUEENSLAND "SCRUB." THE BOTANIC GARDEN.

Members proceeding to Brisbane found a long list of one- and two-day excursions arranged for them. These included among others a visit to the Prickly Pear Experimental Station at Dulacca where Dr. Jean White is conducting experiments for the eradication of the Prickly Pear pest in Queensland': an expedition to the Glass House Mountains (so named by Captain Cook) and another to the Blackall Range and Nambour, an opportunity being afforded on the last-mentioned trip of inspecting a Queensland sugar mill in full working order. A full week-end, however, would allow one to reach and explore a beautiful bit of typical Queensland "scrub" on Mount Tambourin, and my choice fell on the longer excursion. The rail journey to Jimboomba afforded a glimpse of the pine-apple farms, and the drive from thence to Canungra gave one some idea of the Australian stock road. At Canungra, at the foot of Mount Tambourin, one of the largest saw-mills in the State was seen at work, and a ride on the saw-mill trolley for some ten miles up into the heart of the scrub was full of interest and novelty, though the nervous traveller will doubtless prefer the return journey when the trolley is loaded, as giving a greater sense of security. At the end of the journey a halt was made for loading. So skilfully do the men handle the gigantic logs that the operation of transferring them from the stagings by the side of the line to the trolleys is accomplished very rapidly. With no other implement than a pole fitted with an iron crook to give a hold, the loading of three trolleys, each with from six to eight of these immense trunks, together with the necessary shunting of the engine to bring the trolleys in position, was accomplished by three men in less than three-quarters-of-anhour.

Seeing this tropical vegetation for the first time one is impressed by the immense height of the trees forming the close canopy far 1 It is estimated that there are thirty million agrees of pear infected lead

¹ It is estimated that there are thirty million acres of pear-infested land in Queensland, and that the invasion of new areas is occurring at the rate of a million acres a year.



overhead, the great variety of species mingled together, the enormous number of epiphytes often forming bushy excrescenses on the branches or trunks of the trees, the many lianes or "vines" with their rope-like stems dangling apparently from the sky, the gloom. the impenetrability, the silence. Animal life seemed strangely absent. We startled a solitary scrub turkey which flew up noisily and disappeared, but we saw little else. In one spot we heard repeatedly the call of the Whip-bird but we caught no sight of them. A preliminary whistle, easy to miss without close attention, is followed instantly by a loud crack like that of a whip lash. An excursion on foot through similar scrub covering the top of Mount Tambourin gave opportunity for examining the vegetation more in detail. Among lianes one of the most characteristic are the socalled Lawyer Canes (species of Calamus, Palmeæ). The long weak straggling stem lies on the ground or on the undergrowth, or hangs down from the branches of trees up which it has scrambled its way. The leaf rachis is armed with curved prickles; prickles also occur on the leaf sheaths and the margins of the leaf segments thus entangling together everything with which it comes in contact, oneself included. A few yards walk off the track in this virgin scrub is sufficient to demonstrate the difficulty of penetrating this jungle vegetation without some implement wherewith to cut or hack one's way through. Another curious Palm seen was the Walking Stick Palm, Bacularia (Kentia) monostachya, with a slender stem 6 to 12 feet high, which is sometimes made into walking sticks. The stems of the Water Vines (species of Vitis) forming less flexible hanging loops or festoons were abundant. They owe their popular name to the fact that, if a length of the stem be cut out and held up, a drink can be obtained by collecting the water which drips from the lower end. In another liane met with the flexibility of the stem is so marked as to have earned for the plant the popular name of "Supplejack." (This was probably Rhipogon album, a genus allied to Smilax). Many examples were seen of "buttress" roots, a formation common here among many tree forms. "Strangling Figs" also abounded, the trunks of the doomed trees serving as supports showing all stages of envelopment by the descending roots of the fig tree. Among other lofty trees which were identified may be mentioned the Moreton Bay or Hoop Pine (Araucaria Cunninghami), a beautiful Eucalyptus with a smooth silver-white trunk (Water or Flooded Gum) and the endemic Castanospermum australe (Leguminosæ). At one spot pods of the last-mentioned tree measuring about 6 inches by 2 inches and containing 1 to 2 large chestnut-like seeds littered the ground. They appeared to have fallen while still closed, and to have dehisced afterwards as they lay upon the ground. The leafy canopy overhead was so distant and so interlaced that it was difficult to know to which of the trees growing around to assign them. The same difficulty confronted one at another point where the pear-shaped hard-fleshed fruits of Sideroxylon (Sapotaceæ) containing beautifully polished seeds like cowrie shells lay scattered about. Epiphytes were to be seen everywhere, Dendrobiums and Platyceriums (Stag's-horn fern) being the most conspicuous. Of other Ferns the Bird's-nest fern (Asplenium nidus), the Hare's-foot fern (Davallia pyxidata) and various creeping Polypodiums (P. serpens, P. confluens) were met with. The stems of these Polypodiums creep from the ground up the tree trunks often for a considerable distance, and form matted coverings of considerable extent.

On both these excursions we were greatly indebted to Miss Hannah, who was then staying at Canungra and who most kindly acted as guide. Her knowledge of the tracks through the scrub and her familiarity with the vegetation enabled us to make the very most of our limited time.

The Brisbane Botanic Garden is pleasantly situated on sloping ground which runs down to the river bank, but with but a single day in Brisbane itself, only a short visit could be managed. It enabled me, however, at least to see some characteristic Queensland types which had not been met with at Canungra, as e.g. the Silky Oak (Grevillea robusta), a tree which sometimes reaches a height of 100 feet, the Queensland Nut (Macadamia ternifolia) another tall Proteaceous tree, and the Bunya Bunya (Araucaria Bidwilli).

The meeting terminated at Brisbane on September 1st, and I realised that I had just lived the most crowded seven weeks of my life—seven delightful weeks providing me with a succession of new sights, new impressions, new experiences, a few of which I have attempted to review here.

CAMBRIDGE,

January, 1915.

THE ALGAL VEGETATION OF SOME PONDS ON HAMPSTEAD HEATH.

By E. MARION DELF, D.Sc.

[WITH THREE FIGURES IN THE TEXT.]

POR some years past, frequent observations have been made and recorded of the almi and recorded of the algal vegetation of a series of ponds on an estate known as Wylde's Farm, adjoining Hampstead Heath. During this period the ponds have altered somewhat both in form and in depth, but this appears to have affected the phanerogamic rather than the cryptogamic vegetation. The ponds are eight in number, and form a chain running from south to north: their bottom is a rich black mud, a foot or more in depth, with a subsoil of typical London clay; the water is somewhat chalybeate, for rusty masses containing numerous iron bacteria are often seen. The largest ponds are from 150 to 250 feet in length, and have a maximum breadth of about 50 feet. In the diagram (Fig. 1) the ponds are numbered for convenience. No. III has a length of 150 feet and is 50 feet across at the widest part, and the others are drawn roughly in proportion. There is a drop in the land-level between some of the ponds, of some three or four feet: these descents (Fig. 2) are banked up with logs, and are often wet with a trickle of running water; they often bear algæ, and are referred to as the "cascades" in this paper.

Ponds I and VIII have been in existence for many years, a ditch formerly running between them; and through this a more or less permanent stream of water ran, partly owing to an underground spring which supplied pond I even in very dry weather. In the winter of 1908—1909, the ditch was enlarged and banked up at intervals, the present series of ponds being thus formed in order to drain the surrounding fields which had been made over to the public.

Occasional visits were made to the ponds in the years 1910 and 1911, but no systematic examination was then undertaken. Considerable variety was found in the vegetation of the ponds. The commonest submerged flowering plants are Elodea, Callitriche, Lemna minor, Potamogeton spp. and Ranunculus aquatilis; the most characteristic marginal plants were species of Juncus, Bidens, Poa aquatica and Poa fluitans. Amongst the algæ, Spirogyra, Mougeotia, and Vaucheria were found in abundance in the months of February

and March, except in ponds I and VIII. Subsequently monthly and often fortnightly visits to the ponds were made, samples of water from specified regions were taken after dredging, and these

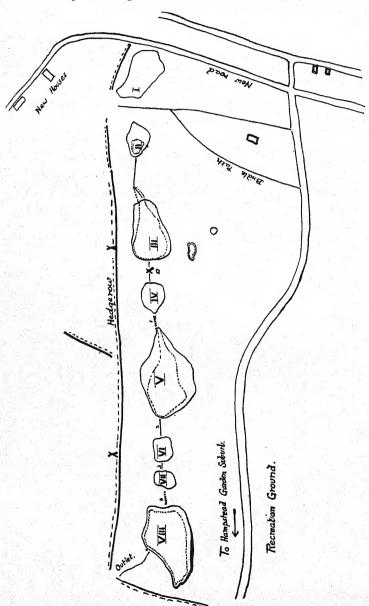


Fig. 1. Chain of ponds on Wylde's Farm, Hampstead Heath, 1912. The dotted lines give the outline in 1913. Trees are marked X.

Algal Vegetation of Ponds on Hampstead Heath. 65

were usually examined at once and recorded in a suitable register. When floating masses of algæ could be seen these were sampled in different parts of the same pond, and the local variations of the same piece of water were sometimes very surprising. Shoots of submerged plants and decaying leaves or stalks were very often examined for epiphytic forms, or for tangled flaments. Frequently the filamentous algæ seem to appear in this manner for a time, and then to gradually increase in amount until at last they float upwards as detached masses often of considerable size. Occurrences of animal and insect life have been noted, but the data are not yet sufficiently comprehensive to be included in the present account.



Fig. 2. Photograph of Cascade II, taken July 8th, 1913.

There is, on the whole, a distinct periodicity in the algal vegetation, the two principal periods being the early winter months (October to December) and the early spring months (February to March or April). The latter phase is the more important, and usually exhibits a predominance of the genera Spirogyra, Mougeotia, Tribonema and Microspora, under the shelter of which a great variety of unicellular and colonial forms occur. The early winter phase is much less distinctive both in variety and amount, but there is no very sharp line between the early winter and the vernal vegetation.

In addition to those algæ which reappear periodically; there are some, such as Scenedesmus, which have only been found

occasionally and sparsely, whilst others, such as Tetraspora and Volvox, appear occasionally but in considerable amount. This spasmodic appearance of one form in abundance is usually limited to a small region of a single pond, so that the causes must be very local as well as of a temporary nature. In the following table of the algæ which have been observed in the whole series of ponds the figures give the number of occurrences noted between January, 1912 and March, 1914, irrespective of the amount observed in any sample: they thus express to some extent, the frequency of any particular form in the ponds.

FLAGELLATA.			ULOTRICHALES.				
Synura uvella Peridinium sp	•••	60 56	¹ Ulothrix subtilis 49 ¹ Microspora floccosa 33				
	•••	21	Draparnaldia) 9 ponds,				
Euglena	•••		glomerata 25 cascades				
Dinobryon sertularia	•••	17	Chætophora risiformis 16				
Ascoglena	•••	16	Stigeoclonium 1				
PROTOCOCCA	LES.		Aphanochæte repens 3				
Chlamydomonas sp.	•••	48	Coleochæte scutata 4				
Carteria		11	STEPHANOKONTÆ.				
Phacotus	•••	7	Œdogonium (2 sp.) 33				
Gonium lacustre		24					
Pandorina	•••	14	,, ciliatum 1				
Eudorina	·	3	HETEROKONTÆ.				
Volvox	•••	9	¹ Tribonema affinis)				
Tetraspora	•••	18	bombycina \ 86				
Palmodictyon	•••	8	Vaucheria sessilis				
Palmellococcus	•••	6	" geminata 4				
Selenastrum		3	Mischococcus 3				
Scenedesmus		12	mischoededs 3				
Characium		7	AKONTÆ.				
Chlorochytrium		1	¹ Spirogyra bellis				
Sphærocystis		20	decimina				
Trochiscia	•••	1	, nitida 106				
Tetraëdon		1	, gracilis				
Chætosphæridium	• • •	3	" sp.?)				
Stipitococcus		1	¹ Mougeotia scalaris)				
Dictyosphærium	•••	2	" parvula?\ 81				

¹ I am indebted to Professor G. S. West for the identification of these species.

Closterium, 2 spp		•••	36	Gomphonema	•••		40
Staurastrum	•••		5	Gyrosigma	•••	•••	7
Penium	•••	• • • •	1	Cocconeis plac	centula	3	3 + 1
BACILLARIÆ.				CYANOPHYCEÆ.			
Navicula sp.	•••	•••	61	Oscillatoria		•••	25
Tabellaria fenestrata 56				Nostoc	•••		8
Synedra radians		46	Lyngbya	•••		4	
,, sp.	•••	}	40	Phormidium s	p.		3
Asterionella	•••		11	Arthrospira	•••		2

For convenience, the occurrence and distribution of these groups will be considered separately.

THE FLAGELLATES.

Synura is undoubtedly the commonest of the Flagellates in these ponds. It has been found at times in every one of the series, but is always more abundant in those with standing vegetation. In pond V, in the region of decaying leaves of Poa fluitans, it has twice been found swarming in the samples collected (February, 1912, March, 1913); it disappears almost entirely in the summer months or may retreat to the deeper water where it would escape detection. Synura is commonly associated with Dinobryon in ponds I, III and V, but the latter is never very plentiful: it also appears somewhat later in the season, and was unusually abundant in pond V in May, 1913.

Euglena has been observed sparsely at intervals in all the ponds and at any time of year, although more apt to increase rapidly in summer. In pond III, on June 18th, 1913, there was a sudden appearance of active Euglenæ over the whole pond colouring the water a bright green. Eleven days previously, careful dredging had revealed no sign of any Euglena, and three days later no green colour could be detected although a fortnight later Euglena individuals were frequent in samples examined. Fritsch¹ concludes that the amount of dissolved substance in the water acts as a limiting factor to the Euglena observed by him in Barton's pond; but in the month of June, 1913, there was a high rainfall², and comparatively poor record of sunshine, so that this theory can hardly be applied to the case of the Hampstead ponds.

¹ Fritsch, F. E., and Rich, F. "British Freshwater Algæ in Nature." Ann. de Biol. lacustre, VI, 1913, p. 64.

² Data of rainfall, sunshine, etc., were obtained from the Meterological Office for an adjoining part of Hampstead Heath.

In December, 1913, a green scum of Euglena formed over the damp mud at the edge of pond II: this has remained for three months without apparent change, but Euglenæ are rarely found in samples of water from the same pond.

Ascoglena has been found in parts of ponds I, III and VII epiphytic on filaments of Tribonema, Mougeotia and Microspora: it is never found on filaments of Spirogyra, present at the same time. It has been found mostly from Pebruary to May; in one case filaments of Tribonema were infested almost at their first appearance with Ascoglena but later on this was in turn almost displaced by numbers of Synedra frustrules.

Species of Peridinium occur very frequently but are seldom found in any abundance. It seems probable that this may be a perennial form, for it has been occasionally found in July and might easily have escaped detection when apparently absent in August and September. Moreover, Peridinium can withstand the extreme concentration of water, and the exposure to sunlight which follows the drying back of a pond even more successfully than such a hardy diatom as Navicula. In June, 1913, pond II almost dried up, a small shallow pool at one end being the only wet part left. No algal vegetation could be detected after careful dredging except the empty frustules of species of Navicula and a few perfectly active Peridinium cells. In the Hampstead ponds Peridinium is distinctly a spring form, becoming most abundant during April and May; the Peridineæ of the Lake District as observed by West and West1 were of general occurrence, but had a distinct summer phase; those of Barton's Pond were found by Fritsch and Rich2 to be most frequent in warmer weather, but according to these authors, a dilution of the water is also favourable.

On the whole, in the Hampstead ponds it may be said that all the Flagellates excepting Euglena are periodically numerous; that Synura and Dinobryon are early spring, and species of Peridinium later spring forms; that Ascoglena depends to some extent on the presence of suitable host plants, especially Mougeotia; and that Euglena is a summer form apt to appear spasmodically in great abundance, but also able to survive winter weather on damp mud in a very sluggish amœboid condition.

¹ West, W., and West, G. S. "Periodicity of the Phytoplankton of some British Lakes." Journ. Linn. Soc. Lond. Bot., XL, 1912.

² Fritsch, F. E., and Rich, F. Loc. cit., p. 54.

THE PROTOCOCCALES.

Of all the Protococcales, Chamydomonas occurs most frequently and often also in great numbers. It reached its maximum in the month of March in the years 1912, 1913, and also in 1914: in each case following a period of considerable rainfall, and slightly rising temperature and sunshine. In ponds IV and VII Chlamydomonas is sometimes accompanied by swarming cells of Carteria, and the latter was found in the same ponds in December, 1913, almost to the exclusion of Chlamydomonas. The Chlamydomonadaceæ die out abruptly in April or linger until May, and in 1913, seemed to completely disappear until the following November. However, in one of the deeper ponds in 1912, a single record was obtained for July, and it is possible that some active individuals may persist even through the whole year in the deepest parts of the water.

Gonium was most abundant from March to April, 1912, in April, 1913, and was found but rarely again in March, 1914. It is therefore a spring form but of distinctly later occurrence than the Chlamydomonadaceæ. Pandorina is a fairly common and Eudorina an uncommon occupant of the ponds, only found from February to May, and much more abundant in 1912 than in 1913. Volvox has been found seldom, but in large numbers. It appeared in a deep corner of pond V which was constantly visited and dredged. On October 17th, 1912, the water from that part was green with Volvox; this condition persisted until November 7th, when daughter colonies were frequent within the mother coenobia, but disappeared shortly after, and excepting for an occasional individual observed in the samples of the following January and February, no other records of this genus have been obtained,

Of the remaining genera of the Protococcales, most were recorded in the year 1912. Tetraëdon, Stipitococcus and Chlorochytrium were found in 1913 but have not been observed since; Carteria, Phacotus and Chætosphæridium have been frequently found in 1913 and 1914 but were absent or (more probably) overlooked in 1912. Tetraspora was unusually abundant in pond V in February and March, 1912, but has scarcely been seen since. Characium is never very abundant but has been found in June, 1912, and in November, 1912 and 1913 on filaments of the larger species of Microspora and Mougeotia.

There is thus considerable variation in the behaviour of the different representatives of the Protococcales, but the majority are early spring forms attaining their maximum development in the

month of March, and disappearing gradually in May and June, 1912, and more abruptly in May, 1913. These months had a nearly equal rainfall in the two years, thus accounting, perhaps, for the longer vegetative period in the former year. The summer temperatures are certainly unfavourable to most of the Protococcales. Very similar results are recorded by Fritsch and Rich for the Protococcales of Barton's Pond, but there the maximum falls later in the spring (April to June). In the Hampstead ponds there is also a secondary maximum in the early winter (October to December): although this is never very striking. Another point of interest is the spasmodic increase of certain genera for unknown reasons; this has been recorded for *Tetraspora*, *Volvox*, *Chlamydomonas* and *Carteria*.

THE ULOTRICHALES.

The commonest and the most abundant members of this group found in the ponds are undoubtedly *Ulothrix subtilis*, *Microspora floccosa* and *Draparnaldia*, but *Chætophora*, *Coleochæte* and others are also present at times. On the whole, there is a well-marked diurnal periodicity, the principal phase occurring from February to the end of April, and the secondary phase occurring from the end of October to December.

The genus *Ulothrix* has been found in greatest abundance during the months of February and March, 1912. It appears to increase in amount either gradually (V, February, 1912) or suddenly (VI, December 2nd, 1913), but in either case is apt to disappear very rapidly (III, V, VII, 1912). The rapid increase is readily intelligible from the ease with which whole filaments break up into zoospores and the abrupt disappearance may perhaps be accounted for by the attacks of water insects, or animals, which are themselves apt to increase rapidly at this time of year.¹

The genus Microspora is more gradual both in becoming dominant and in disappearing. It is, on the whole, a later spring form than Ulothrix, becoming dominant in March and April, 1912, in most of the ponds and in two cases even persisting into June and July. In a recent paper, the periodicity of another species of Microspora is fully discussed by Fritsch,² and he concludes that the principal factors which condition its dominance in Barton's Pond,

¹ Tadpoles were numerous in ponds III and VII in May, 1913. In their early stages these are voracious vegetable feeders, and this may account for the abrupt disappearance of both the Protococcales and the Ulothricales in that year.

² Fritsch, F. E., and Rich, F. Loc. cit., pp. 30-35.

near Harpenden, are (1) a relatively low temperature of the water (2) absence of competition between it and two other filamentous algæ, Œdogonium and Conferva. In the Hampstead ponds, however, a low temperature does not seem to be a determining factor, for the amount of Microspora present in ponds IV and VII increased during a steady rise of mean temperature throughout March and April, 1912, and in ponds I, III, IV and VII filaments were present in more or less abundance, in May and June of the same year at still higher temperatures. In July, 1912, there was an unusual abundance of Microspora in pond VII in spite of a very high mean temperature. On the other hand, in October and November, 1913, Microspora has been found in pond III during weeks when the temperature had been steadily falling. With regard to the competition factor, however, my observations, in the main, bear out those of Fritsch. The period of greatest abundance of Microspora is before that of the dominance of the Conjugatæ; as the Conjugatæ increase, Microspora decreases in amount; towards the end of July, 1912, when there was a local abundance of Microspora in pond VII, the Conjugatæ had already entirely disappeared. On the other hand, Ædogonium though present, never appears to compete successfully with other forms in these ponds, and Tribonema has maintained itself successfully during the whole of the periods during which Microspora has flourished, but neither appears to have impaired the other.

Draparnaldia has been of frequent occurrence, but is most abundant in the cold weather. It has been found attached by a network of rhizoids, to sunken logs of wood, to the submerged roots of grasses and other aquatics, and once forming an extensive beard upon the back of a snail (Limnea sp.). It appears and disappears abruptly as does Ulothrix, and on the logs of the cascades is often associated with Chætophora, or with Vaucheria. In the former case, Draparnaldia appears to gain the ascendancy, and crowd out the Chætophora; in the latter case Vaucheria with its dense matted filaments often suppresses the Draparnaldia.

THE STEPHANOKONTÆ.

This group is principally represented in the ponds by two species of $(Edogonium)^1$ one of which was observed to form oospores in June, 1912, but not in abundance. It has rarely been found to predominate in the vegetation of any pond, though it was dominant

A third species, Œdogonium ciliatum, has been seen once only.

locally in VII (February, 1912), and in I (June, 1912). It has diminished markedly in amount during the whole of 1913, although it has often been found as part of the soft scummy matter which collects around the stems and leaves of submerged aquatic phanerogams, and frequently as a number of sporelings attached to the surface of some submerged object.

Œdogonium was most abundant in these ponds in 1912, during the dominant phase of the Protococcales, Flagellata and Ulothricales. According to Fritsch,1 it tends to predominate during warm weather and bright sunshine in the Barton Pond, but in the Hampstead ponds it was most abundant in the colder months of the year (January to March), although the fruiting period (June, 1912) was a period of unusual warmth, and moderate rainfall and sunshine. In several cases, when samples of the algal flora of one of these ponds have been kept under observation for a number of weeks or months, Ædogonium was ultimately found to dominate every other filamentous form, although scarcely to be found at first. On February 26th, 1912, a sample of water from pond III was found to contain principally Spirogyra and Ulothrix, but also a very little Edogonium, Mougeotia, and a few of the Protococcales. It was placed in a large glass jar with plenty of water, and examined some months In July the Protococcales had disappeared, as well as Ulothrix: the original species of Spirogyra (S. bellis) had persisted, but two other much smaller species had also established themselves. In the following January, an examination of the same jar shewed that the Spirogyra had been entirely replaced by the Edogonium which had been present in small amount from the first. observations suggest that Edogonium suffers from competition, especially with the Conjugatæ; but from some other observations on Edogonium during zoospore formation, it seems probable to me that the large zoospores, and even the young filaments, are often eaten by such aquatic insects as Asellus, which is an inhabitant of all the ponds. It is not possible to account for the entire lack of a fruiting period in 1913 as compared with 1912.

THE HETEROKONTÆ.

Two species of *Tribonema* occur, of which *T. bombycina* is by far the commonest. The records apply mainly to this species, which is, however, sometimes accompanied by *T. affinis* in smaller amount. *Vaucheria sessilis* and *V. geminata* have both been observed,

¹ Fritsch, F. E., and Rich, F. Loc. cit., pp. 26-30.

but the former is the commoner. Michococcus is a small epiphytic species which has only been seen in February, 1914.

On the whole the Heterokontæ show the same well-marked dominance in the vernal phase (February to May), but *Tribonema* persists in small amount almost throughout the year as a slight tangle of filaments around submerged plants in a way which suggests that it is probably perennial. When on the increase, the filaments appear to multiply freely, appearing at first as little flocculent masses around various submerged shoots—especially around *Elodea*. A little later soft pale green masses are found freely floating in the water, as has been seen in ponds I and IV, February and March, 1912, and in V locally, in October to December, 1913.

According to Fritsch, Tribonema flourishes best in the absence of sunlight, but is sensitive to competition, especially with Microspora. My observations bear out the shade-loving habits of the plant, for it is always most abundant in those regions in which it is sheltered by submerged vegetation. Although most abundant in the comparatively dull months of February and March, it was yet common in ponds V and VII in June, 1912 and in May, 1913, these two ponds being deep in parts, and having many aquatic phanerogams, both marginal and submerged. In my experience there is no evidence that Tribonema suffers at all seriously from competition with either Microspora or any of the early spring filamentous algæ. In the Hampstead ponds, however, it is apt to suffer from attacks of epiphytes, especially from Ascoglena and from species of Synedra and Gombhonema; these epiphytes become especially numerous towards the end of a period of vegetative activity of Tribonema, the Ascoglena in the colder, and the Synedra in warmer weather. On the whole, in these ponds, Tribonema may be described as a probably perennial form with a well-marked maximum in February and March, and with a less distinctive secondary maximum in October and November.

Vaucheria has been observed mostly on the logs which form the small cascades from one pond to another, attached firmly by numerous rhizoids to the somewhat sandy crevices of the wood. In April, 1912, V. geminata was found fruiting amongst matted filaments of V. sessilis. In February and March, 1913, V. sessilis was again found fruiting freely, but V. geminata was not seen. When the cascades dry up for a few days or weeks, the Vaucheria seems to disappear. Three or four days after the flow of water is resumed, Draparnaldia is commonly found, which is quickly followed,

and in summer almost entirely replaced, by Vaucheria. On the cascades fruiting specimens have been obtained in the months of February, 1912, and in July and December, 1913. In the ponds V. sessilis has been found, both in February, 1912 and in December, 1913, but it is much less common than on the cascades. There is thus no evidence for periodic activity in this form, which appears suddenly, persists for a lodger or shorter time, and disappears abruptly: on the whole, however, it prefers the colder months.

THE AKONTÆ (CONJUGATÆ).

The Conjugatæ are perhaps the most characteristic of all the green algæ of the ponds, appearing in great quantity from March to June, and in considerable amount in the late autumn months also. Mougeotia is the dominant form in ponds I and II, and has occasionally been locally abundant in V; various species of Spirogyra are also abundant, especially in ponds III, IV, V and VII. Desmids are never abundant, but Closterium has been found in every pond as an occasional constituent; Staurastrum has sometimes, and Penium very rarely, been seen. The occurrence of these genera will be considered separately.

Several species of Spirogyra are present in the ponds, but only two have been observed to conjugate in nature; S. decimina and S. bellis. Both of these have been found in great quantity, forming large sheets of submerged green on the bottom of the pond, as in III (November and December, 1913), or floating in tangled masses over the surface of the water as in March to June, 1912. Two other species of Spirogyra have been observed, S. gracilis and S. nitida, the latter having once been seen to conjugate in a culture solution in the laboratory. These two species occur frequently but never in any abundance. There is a certain amount of constancy in the distribution of these four species. S. decimina and S. nitida are characteristic of ponds II and III, and S. decimina has also once been found in pond VIII (October, 1913). S. bellis, on the other hand, is constantly found in another part of pond III, and in ponds V and VII; the species do not seem to intermingle but occur in patches, side by side.

The vegetative period of all the species fell mainly in March, April and May in 1912, followed by the fruiting period in June and early July. The first signs of conjugation were observed in the last week of May (ponds III, IV, V and VII), when the green slippery masses floating on the surface began to appear tangled

and slightly brown. About ten days later the green zygotes began to turn brown and to sink, so that it became possible to distinguish two strata,—an upper green one where conjugation was still at its earliest, and a lower brownish one where the zygotes were nearly ripe. Later on the zygotes could be detected in the mud at the bottom of the pond (July, 1912, pond II).

The different species of *Spirogyra* seemed to wholly disappear from the ponds during the months of July, August and September, both in 1912 and 1913. In each case they reappeared towards the end of October, at first as a few scattered filaments clinging around

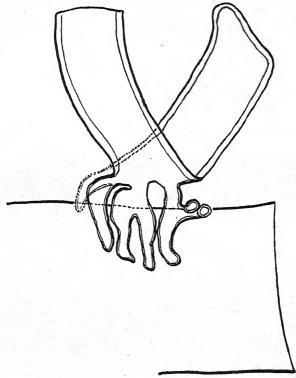


Fig. 3. Spirogyra (? adnata), showing haptophores clasping a filament of Vaucheria. Drawn with Zeiss $\frac{1}{8}$ lens.

submerged vegetation, although not actually attached to it. Later in the winter the filaments increase in length and in numbers, and cell-division becomes active, especially after a hard frost; but the filaments never become as numerous as in the spring months when they dominate the whole of the algal vegetation, I have repeatedly observed that young tadpoles, snails, aquatic insects such as Asellus, and various aquatic larvæ, will not touch any species of Spirogyra

for food, although they speedily demolish all signs of *Œdogonium*, *Ulothrix* and various other green algæ: this may perhaps account for the ease with which this genus persists through the months of April, May and even June, when these ponds are teeming with the most diverse animal life.

A peculiar species of Spirogyra has been observed attached to the logs of one of the cascades. In spite of many observations in the field and numerous culture experiments, it has never been found in conjugation, but the sterile filaments closely resemble those or S. adnata. This is distinctly a summer form and has only been found from July to November, 1912, and very scantily in June and July, 1913. It was most abundant in July and August, 1912, and disappeared entirely in December of that year, being apparently suppressed by a luxuriant growth of Draparnaldia. The filaments are curious in being attached to the substratum by much branched rhizoids, which become very stout and thick. In one case a filament was found the rhizoids of which had clasped a neighbouring filament of Vaucheria with many delicate finger-like processes (Fig. 3); in other cases the central cells of a filament were fastened down by rhizoids, the two ends trailing freely in the running water.

The seasonal activity of Spirogyra has been fully discussed by Fritsch.2 According to this author, there is usually a well-marked vernal phase in the later spring months, a more or less complete disappearance of the filaments in the summer months and a secondary autumnal activity in some cases (e.g., in Abbot's Pool), probably whenever the summer conditions allow a few vegetative filaments to persist unharmed. In the Hampstead ponds most of my observations are in accord with these views. There has been a late autumn or early winter period both in 1912 and 1913, but never as well-marked as the spring maximum. In 1912 there was a long and striking vernal phase, but the autumn phase was insignificant; in 1913 the vernal phase was much less striking than in the preceding year and no conjugation was observed in the ponds, although zygospores were easily produced in the laboratory from the same material in May and June. The following autumn the filaments reappeared in October (ponds II, III and IV), in November (V and VIII) also in December (I and VI), and conjugation was observed on a bright

¹ See Delf, E. M. "On an attached species of Spirogyra." Annals of Botany, 1913.

² Fritsch, F. E., and Rich, F. "Preliminary observations on Spirogyra.' Annals of Botany, 1907; "Five years' Observation of Fish Pond, Abbot's Leigh." Bristol Nat. Soc., 4th ser., II, 1909.

day in October in S. decimina (pond II), but the zygotes never ripened and all the filaments soon disappeared. The only species which could survive the summer without apparent harm was S. adnata in 1912. As in the species discussed by Fritsch, the Hampstead Spirogyras appear to thrive best in the bright days following heavy rainfall in the late spring or early summer.

The genus Mongeotia has been represented at some time or other in every pond, but never occurs in such abundance as does Spirogyra. It is throughout represented by two forms, a large one which has never been seen to conjugate (probably M. scalaris) and a much smaller species which conjugated to some extent in June. 1912. In ponds I and II these species together dominated all of the other green algæ from April to July, 1912, and from February to June in 1913. In all the other ponds Mougeotia is distinctly secondary to Spirogyra, appearing later, and disappearing earlier: it also exhibits a distinct autumn phase. In both of these respects the Mougeotias of the Hampstead ponds differ from those observed by Fritsch, which were more hardy, appearing first, and lasting longer than Spirogyra; these also had a less decided autumn phase than the associated Spirogyra.

The desmids are represented by the three genera Closterium, Staurastrum and Penium. Of these, the first has been found in every pond excepting pond I, and at every time of year excepting August and September. It is never abundant, but reaches a slight maximum from March to May, i.e., rather earlier than the accompanying Zygnemaceæ. In Barton's Pond! the maximum development of Closterium was in early summer, following the filamentous Conjugatæ; and in the lakes of the north-west of England, Closterium and other Desmidiaceæ were most frequent in the latter part of the year (June to November). Their occurrence is thus variable, and probably the result of local climatic effects.

On two occasions when samples of algæ from the Hampstead ponds were kept for months in a large glass jar of water, all the animal life, and finally all the plant life, excepting desmids, disappeared. At first a mixture of the three forms was found, but ultimately *Penium* dominated the rest, and appears to be able to last for months unchanged. It seems to me probable that the presence of animal life may well act as a check on the increase of these desmids in nature, for I have more than once observed one

¹ Fritsch, F., and Rich, F. Loc. cit., pp. 23-26.

West, W., and West, G. S. Loc. cit.

of the larger microscopic worms digesting a plant of *Closterium* nearly half the length of its own body, as well as various diatoms and unicellular green bodies which must have been either *Chlamydomonas*, or zoospores of about the same size; these worms are very numerous in the Hampstead ponds.

THE BACILLARIÆ.

These form one of the most characteristic features of the vegetation of the ponds. They are probably present all the year round, though much diminished in the summer months, and they have a marked vernal maximum from February to May, when they form delicate brownish strands around any submerged plants, but particularly around *Elodea* and the old decaying leaves of *Poa fluitans*.

The genus which is most widely distributed is undoubtedly Navicula, especially a small species, which abounds in the mud of all the ponds. Gyrosigma has been found in ponds II and VIII, and is also a mud-loving diatom. Tabellaria fenestrata is very abundant as well as of frequent occurrence, but is principally epiphytic in habit; Synedra is also very common and is either free-swimming or epiphytic in habit.

There is a certain amount of difference in the diatomic flora of the ponds. Tabellaria is characteristic of ponds I, III, IV and V, and infrequent or absent in the rest; it is associated with Elodea in the first three and with Poa fluitans in the last of these ponds. Synedra is particularly common in ponds III and IV, although found more or less frequently in all the ponds. Gyrosigma and Gomphonema are mostly found in ponds II and VIII, although also seen occasionally in other ponds. Cocconeis has been observed epiphytic on Microspora, Tribonema and Vaucheria, principally in pond V.

Most of the diatoms of the Hampstead ponds are spring forms, dominant from February to May (1912, 1913, 1914), with a slight secondary maximum from October to December (1912), or in December (1913). They seem to disappear wholly in summer, although some may prove to be perennial on closer investigation. Tabellaria fenestrata (and perhaps also Synedra) seems to be associated with phanerogamic rather than filamentous hosts. Both of these diatoms reach their maximum during the colder months of winter or early spring, when the decay of the previous year's vegetation is in an advanced state; at the same time, these are usually rainy months, so that a supply of nitrogen from decay, and

Algal Vegetation of Ponds on Hampstead Heath. 79

also the æration and dilution effected by a good rainfall, seem to favour the development of these forms. Navicula persists into the summer months although possibly disappearing in July and August.

There is little comparative evidence as to the periodicity of diatoms, but the above remarks shew that there is a general resemblance between the diatomic flora of the Hampstead ponds and of Barton's Pond.¹ On the other hand, in the lakes of the north-west,² West and West found that the Bacillariæ were principally autumn forms, sometimes shewing summer maxima.

THE CYANOPHYCEÆ.

This group is chiefly represented by the genus Oscillatoria, but Nostoc, Lyngbya and Arthrospira have also been seen. The occurrences are somewhat irregular, but all fall within the colder months of the year. Nostoc has been recorded for October, 1912, and for February and March in 1912 and 1913. The remaining genera have only been found in the months of February and March and are never very constant constituents of the samples obtained. It is probable that they are inhabitants of the deeper water, possibly on the mud floor, and so frequently escape detection.

SUMMARY AND GENERAL CONCLUSIONS.

There is a well-marked periodicity in the occurrence of the majority of the algæ in the ponds on Hampstead Heath. The season of greatest diversity and abundance was from February to April or May in the years recorded. This corresponds to a period of variable rainfall, gradually ascending temperatures, increasing light intensity, and of comparatively slight development of animal life. The rainfall is probably less directly influential in these ponds than in some, for there is usually a good supply of water from underground sources. As the temperature rises from May to July the algæ become greatly diminished, and many forms altogether disappear until late in the following October, or early November. They reappear first in those ponds which are slightly warmer and bear more phanerogamic vegetation and about two or three weeks later in the remaining ponds (I, II, VI and VIII).

In 1912 there was a secondary maximum in October and November, falling off again in December and January, but in 1913

¹ Fritsch, F. E., and Rich, F. Loc. cit.

² West, W., and West, G. S. Loc. cit,

there was a slight increase in December and an apparently stationary condition in January prior to the early vernal maximum (January to March) which followed.

The Protococcales and Ulotrichales are dominant somewhat prior to the Conjugatæ and Heterokontæ, the Conjugatæ dominating every other form in April and May. One species of *Spirogyra* has been described which is apparently a summer form.

Some attempt has been made to elucidate the complex causes underlying the distribution and periodicity; but our knowledge of the habits of most of the algæ is too limited to throw very much light on such problems. Further observations are in progress with a view to obtaining more detailed information on various points.

In conclusion, I have to acknowledge the valuable help of Miss Winifred Blackwell, formerly a student of Westfield College, in collecting and examining some of the samples of 1912. I am also indebted to her for one of the July records of 1913. My thanks are also due to Professor G. S. West for kindly looking through some of the material, and for identifying the species of Spirogyra, Microspora, Ulothrix and Tribonema recorded.

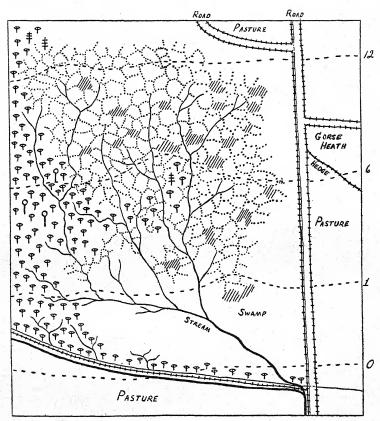
A SOMERSET HEATH AND ITS BRYOPHYTIC ZONATION.

By W. Watson, B.Sc.
[With Seven Pigures in the Text].

I. Introduction.

WET heath association is well shown on a portion of Chard Common in South Somerset. The dominant vascular plants are Molinia cœrulea, Erica tetralix and Myrica gale, and these occur in a field of about 3 acres (1.2 hectares) on siliceous Mid-Lias beds, the field having an altitude of about 350 feet (106 metres) above sea-level and a fairly regular slope of about 1 in 30). Along two sides of the field there runs a stream fed by many small tributaries, which in turn are fed by the water from the furrows between the Molinia tussocks so that a network of small potential

islands is formed (Figs. 1-3). The tussocks vary from a few centimetres across to more than a metre, the height varying from a few centimetres to a half-metre in extreme cases; while the furrows separating them are intermittent or continuous channels of water, and in the latter case may be 50 cm. wide and deepened by erosion, but the ultimate ones are usually less than 15 cm. in breadth. and



9 ALDER. P. BIRCH. FOAK. M LARGER SPHAGNUM POCKETS.

Fig. 1. Diagrammatic sketch-map of the heath. The furrows between the *Molinia* tussocks are represented by dotted lines, the size of the tussocks being exaggerated. The lowest portion of the heath is shown by the contourline marked 0, the actual height above sea-level being approximately 350 feet (106 metres); the other contour lines indicate the increase in height in feet from this zero line. The stream and its tributaries are indicated by continuous lines. The road by the side of the heath is bounded by hedges which are represented by crossed lines. Scale 1 in 1000.

are often very shallow. During wet weather the whole field is very wet, but after a period of drought the *Molinia* tussocks become dry and are separated by damp furrows. Under ordinary moist climatic

conditions most of the interlinking furrows have a thin basal layer of water, the depth varying according to fluctuating conditions and undulations of the ground.

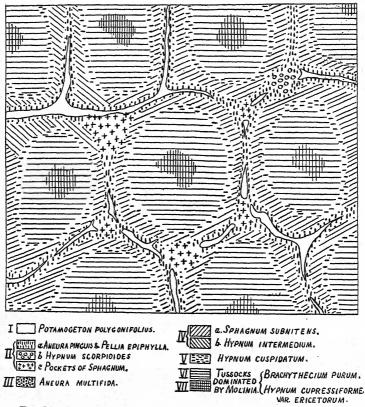


Fig. 2. Sketch-chart of a portion of the heath showing the distribution of the bryophytic zones. The double lines enclose channels of open water during moist weather conditions. Scale 1 in 50.

The lower and flatter portion of the field is less definitely mapped out into intersected areas (Fig. 1), is often swampy and local societies of Hypericum elodes, Menyanthes trifoliata, Mnium affine (the form often known as var. elatum), and Bryum pseudotriquetrum may occur in a matrix of Hypnum cuspidatum, H. stellatum, H. intermedium, H. giganteum and Sphagnum spp., with an abundance of Hydrocotyle vulgaris, Galium uliginosum and Anagallis tenella.

The surrounding fields have been drained and are used for pasture, except on one side where the triangular apex of a dry heath almost abuts on the wet heath (Fig. 1). On this dry heath gorse

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is very abundant and is associated with Calluna, Pteris and other plants characteristic of a dry heath association. On the opposite side the wet heath merges into an Alnus thicket.

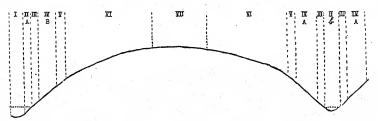


Fig. 3. Diagrammatic section showing the different zones, except a "pocket" of Sphagnum cymbifolium (II C). The horizontal dotted line represents the general level of water under moist weather conditions. Scale 1 in 20. (II b on the right should be II B).

A certain amount of shade is given to the herbaceous plants by the presence of *Myrica gale* and an occasional alder (*Alnus glutinosa*) or willow (*Salix cinerea*), and for the smaller ones the rank-growing grasses and other vegetation provide not only shade but such severe competition that only a relatively small number of

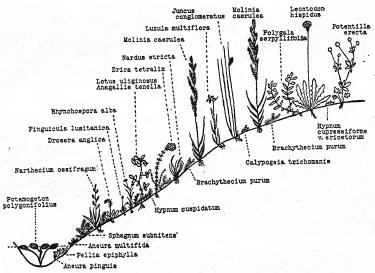


Fig. 4. Section through a water channel and a tussock. Scale 1 in 10. The section passes through a zone of Sphagnum subnitens.

species occurs. This shading often gives a drawn-out appearance to the plants, and especially to the bryophytes which will be mentioned later.

^{1 &}quot;Types of British Vegetation," p. 107.

Few fungi and no terricolous lichens were noticed on the heath itself, though the former were abundant in the adjacent Alnus thicket, Boleti and Russulæ being especially noticeable. The only fungus noted as occurring on the Molinia tussocks was Laccaria laccata, but no particular search was made for these plants.

11. ZONATION OF THE VEGETATION.

The zonation of vegetation from the wet to the drier and more exposed positions is evident by the distribution of the vascular plants, but is shown in greater detail by the bryophytes. On taking these non-vascular plants into consideration, seven zones can be distinguished, and each of these, with the exception of the first, is characterised by the presence of a particular bryophytic species (Figs. 3, 4, 5).

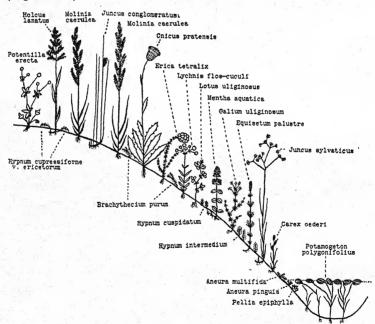


Fig. 5. Section through a wide water-channel and one of the highest tussocks. Scale 1 in 10. The section passes through a Hypnum intermedium zone.

I. Zone of Potamogeton polygonifolius. In the small tributaries or furrows where water is constantly present Potamogeton polygonifolius is abundant, in fact it is the only plant evident when the water is more than 10 centimetres deep. Frequent examinations of the stream-bed showed that no vascular plant or even a characeous or

bryophytic one was present, though desmids were very abundant and characteristic.1 Towards the edges of the stream other plants were found and it is purposed to take this as the more common facies of the second zone.

II. The second zone is characterised by three alternating facies each dominated by a distinct species of bryophyte, and called here II A.

The following plants are found in this second zone:-

Potamogeton polygonifolius o Aneura pinguis a Hypnum scorpioides Id revolvens o

Hydrocotyle vulgaris f Pellia epiphylla a Sphagnum cymbifolium Id

stellatum o

" v. squarrosulum o recurvum la

Aulacomnium palustre a

rufescens o

II A. Facies of Aneura pinguis and Pellia epiphylla. The first plants, apart from the algæ, to relieve the isolation of the pondweed are the two thalloid anacrogynous Jungermanniales, Aneura pinguis and Pellia epiphylla. These are the dominant plants, not only at the margins of the zone of Potamogeton polygonifolius but also in the moist furrows where that may be absent. Both are variable, the thalli often becoming long and narrow, especially in Aneura pinguis which becomes very like Pellia in appearance (Fig. 6). Many of the Pellia plants are almost typical, but typical specimens of Aneura pinguis are seldom met with. This is correlated with the fact that the habitat is much nearer to the usual one for the Pellia than for the Aneura. Hydrocotyle vulgaris is occasionally present, but is more abundant in the swampy (lower) portion of the heath.

II B. Facies of Hypnum scorpioides. In some places small shallow boggy pools are formed, and in these the Aneura and Pellia are usually absent, little vegetation of any kind occurring save the characteristically reddish Hypnum scorpioides, accompanied by a little H. revolvens and less frequently by H. stellatum. During dry weather these areas become patches of moist peat and H. stellatum then often shows a distinct secundity of its leaves.

II C. Facies of Sphagnum cymbifolium. In other cases these depressions form pockets of Sphagnum, especially S. cymbifolium and its colour variety glaucescens. When a fair amount of shade is afforded by Myrica, etc., the pockets chiefly consist of S. cymbifolium var. squarrosulum, which is characterised by having the leaves spreading out in a squarrose manner, thus compensating for

¹ Cf. G. S. West in Types of British Vegetation. p. 193.

the reduced amount of light. Aulacomnium palustre is abundant amongst the Sphagnum and is usually very slender and elongated with smaller leaves and fewer rhizoids than in the type. At the edges of the Sphagnum pockets, where it is less shaded and more liable to desiccation, it becomes more typical, being three to four times as broad and having numerous rhizoids.

The alternation of these three facies seems to depend on the supply of fresh water. Where the water is continually being replaced Aneura pinguis and Pellia epiphylla (II A) are present, but when the water supply is intermittent and the water settles for some time the other facies of this zone are shown. The relations between the pockets of Sphagnum cymbifolium (II C) and the patches of Hypnum scorpioides (II B) are not so definite, and the uncertain evidence is not altogether en rapport with what has been observed in other The pockets of Sphagnum cymbifolium are formed in depressions which are nearly always wet, and sometimes a metre broad, whilst the Hypnum scorpioides occurs in smaller patches in shallow peaty pools, the surfaces of which are above those of the interlinking channels, are liable at times to become flooded and in times of drought become dirty patches of moist peat which often coats the Hypna so thickly that they are scarcely distinguishable. The infrequency, smallness and indistinctness of these areas render a more definite correlation with the pockets of Sphagnum difficult. When the pockets consist of S. recurvum, as is not infrequently the case, they are more constantly wet than when formed of S. cymbifolium.

III. Zone of Aneura multifida. The sides of the furrows just at the water-level are occupied by a very definite line of this thalloid liverwort with scarcely any admixture of other plants. It occurs immediately above the Aneura pinguis and Pellia zone (II A), and may even extend downwards into it, in which case the thalli change in character, becoming longer, narrower and less branched owing to their more aquatic and shady positions (Fig. 6 E). Where the facies of Hypnum scorpioides (II B) or of Sphagnum cymbifolium (II C) occurs, Aneura multifida may form the next zone in a wet to dry succession, but is not so definite as when it abuts directly on the Aneura pinguis and Pellia epiphylla facies (II A). The hepatic sometimes extends into drier zones and then becomes more tufted in character (Fig. 6 G). So far as it is at present known, this district is the only one in S. Somerset where A. multifida (so characteristic of the sides of moving water in uplands) occurs.

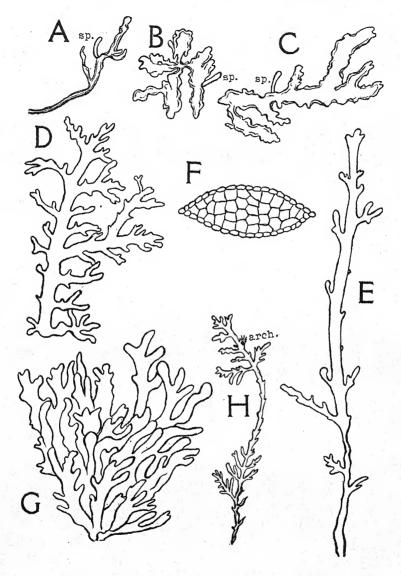


Fig. 6. A—C, Aneura pinguis (L.) Dum.:—A, plant growing in the water; B, plant from a moist fallow field, Aisholt, Somerset; C, plant of a fairly typical character. D—H, Aneura multifida (L.) Dum.:—D, type from side of a mountain stream, Edale, Derbyshire; E, drawn form from the heath, Chard Common; F, transverse section of the middle portion of E (the marginal layer is one cell thick and often consists of 2-3 rows of cells in typical plants, and the thicker postion of the thellar of the transverse of 6.7 cells). C and the thickest portion of the thallus often consists of 6-7 cells); G, tufted form from the heath, Chard Common; H, a fairly typical form from same locality (the branches in the middle portion have not developed owing to the competition of surrounding plants). Arch., archegonial branch; sp., sporogonium-containing calyptra. A-C, \times 2; D, E, G, \times 6; F, \times 60; H, \times 3.

IV. The fourth zone is characterised by two alternative facies dominated by distinct species of mosses. The dominant moss by the margins of the smaller channels is Sphagnum subnitens, but by the sides of the more definite tributaries where there is a slow but constant current, it is almost entirely replaced by Hypnum intermedium; one of the reasons for this is that the latter moss requires a more constant water-supply, as it is not adapted to take up such a large amount of water when it is available as the former.

IV A. Facies of Sphagnum subnitens. Immediately above the Aneura multifida zone, about 2 cms. above the general level of the water, various species of Sphagnum appear. The dominant one is S. subnitens, especially its colour-variety violascens, but other Sphagna are also present. Cephalozia connivens is usually intermixed with the shoots of the Sphagnum, and Calypogeia fissa is also abundant, the latter being often very much drawn and with small leaves decurrent to a considerable extent when shaded by a quantity of overlying Sphagnum, and in this condition is a form analogous to the var. aquatica of C. trichomanis (Fig. 7 B). Pinguicula lusitanica, Narthecium ossifragum and all three British species of Drosera are frequent—D. rotundifolia is the most frequently noticed, not only on account of its relative abundance, but also owing to its more superficial position.

The plants occuring in this facies are as follows:-

Viola palustris f
Hydrocotyle vulgaris f
Pinguicula lusitanica o
Scutellaria minor o
Narthecium ossifragum f
Sphagnum subnitens d
" rufescens f
Calypogeia fissa a

Drosera anglica f
" rotundifolia a
" longifolia f
Mentha aquatica o
Rhynchospora alba o
Hypnum intermedium o
Cephalozia connivens a

IV B. Facies of Hypnum intermedium. Sometimes the Sphagnum subnitens facies is not well marked, or it may be replaced by a zone in which species of Hypnum are abundant, this being especially well-shown by the sides of slowly running water. The floristic composition of this facies is shown in the following list:—

Viola palustris f
Pedicularis palustris f
Hydrocotyle vulgaris a
Galium uliginosum a

" var. Witheringii I

" palustre I Mentha aquatica a Narthecium ossifragum f Glyceria plicata I
Equisetum maximum o
(a in or near alder thicket)

" palustre a " var. polystachyum o " limosum I

Sphagnum subnitens o

Juncus sylvaticus a
Eleocharis multicaulis o

Carex paniculata I

pulicaris o fulva o

echinata o

Hypnum intermedium d

" giganteum f " scorpioides form o

H. revolvens f

H. cuspidatum o
Mnium affine var. elatum o

œderi a Bryum pseudotriquetrum o

The dominant Hypnum is Hypnum intermedium, but it is often associated with other Hypna, these associates forming a mossy carpet in which the vascular plants are sprinkled. H. cuspidatum and Mnium affine var. elatum may occur, but they are more frequent in a slightly higher zone or in the flatter lower portion of the heath.

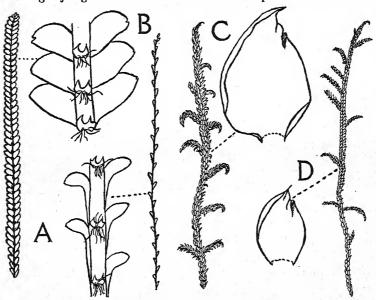


FIG. 7. A, B, Calypoegia fissa (L.) Raddi, two plants from the heath—A, a nearly typical plant though rather elongated; B, a slender form found in shadier and more aquatic situations. C, D, Hypnum scorpioides L.:—C, typical plant with a reddish colour, from II C.; D, slender green form from IV B. (see Text). Plant in each case $\times 2$; part of plant, or leaf, $\times 15$.

H.giganteum, which bears a superficial resemblance to H.cuspidatum but has nerved leaves, occasionally forms an outward fringe to the H.intermedium. The form of H. scorpioides occurring in this zone (Pig. 7, D) differs from the normal plant found in II B in the more erect habit, the slenderer shoots, the smaller, greener and less rugose leaves and seems to be a state due to severer competition and reduction of light by its associates.

V. Zone of Hypnum cuspidatum. This is seldom distinguishable from the last zone, but sometimes the Hypnum cuspidatum

forms a fairly definite border. H. stellatum appears to belong to the same zone; it may be intermixed with either H. intermedium, H. giganteum or H. cuspidatum, but sometimes occurs on drier ground than any of these. As is the case with H. cuspidatum it is commoner in the flatter portion of the field than between the Molinia tussocks. Sphagnum subsecundum occasionally becomes dominant in this zone and is intermixed with Calypogeia trichomanis.

In this zone we find the following plants:-

Lychnis flos-cuculi f
Lotus uliginosus f
Lythrum salicaria o
Epilobium palustre a
Cnicus palustris f
" pratensis f
Erica tetralix d
Anagallis tenella sd
Orchis latifolia o

O. ericetorum o
Carex helodes I
(chiefly near thicket).
Equisetum palustre f
"maximum I (shaded places)
Sphagnum subsecundum Id
Hypnum cuspidatum d
"stellatum a
Calypogeia trichomanis f

VI. Zone of Brachythecium purum. Where the dominant vascular plant is Molinia cærulea the ground, though damp, yields few bryophytes, the competition of the grass being too severe. The floristic composition of this zone is as follows:—

Lychnis flos-cuculi o
Lotus uliginosus o
Angelica sylvestris f
Genista anglica o
Rubus idœus I
(in or near thicket)
Eupatorium cannabinum o

" pratensis o
Erica tetralix o
Habenaria bifolia I
Luzula multiflora a
Juncus effusus a

Cnicus palustris o

" conglomeratus a

Molina cœrulea d Agrostis canina f Nardus stricta f Sphagnum papillosum If

,, var. confertum If

yar. purpurascens o
Brachythecium purum a
Hypnum cupressiforme var. ericetorum (drawn form) o
Aneura multifida (tufted form) o
Cephalozia connivens o
Lophocolea bidentata o
Calypogeia trichomanis o

The only moss present in abundance is Brachythecium purum but sometimes the colour-variety purpurascens of Sphagnum subnitens is frequent. Intermingled—with the lower portions of this and therefore in a more protected habitat, is Cephalozia connivens, whilst on the surface a somewhat tufted state of Aneura multifida (Fig. 6, G) is present, the crowded thalli protecting each other against the unusual evaporation to which they are exposed. Sphagnum papillosum, and especially its variety confertum, also occurs, the crowded and congested character of the variety enabling it to live in a drier situation than the type. Very complanate and green forms of Hypnum cupressiforme v. ericetorum with well-developed auricles also occur.

VII. Zone of Hypnum cupressiforme v. ericetorum. In the driest portions of the tussocks bryophytes are scarce, the only one which occurs with any frequency being H. cupressiforme and its variety ericetorum. Molinia carulea is the dominant vascular plant but many invaders occur and are often "drawn" owing to the shade of the Molina and the overspreading Myrica. A definite species of Rubus with long trailing stolons is frequently present.

The following list shows the chief plants found in this zone:—

Polygala serpyllacea f
Hypericum humifusum o
" pulchrum o
Linum catharticum o
Potentilla erecta a
Rubus sp. f
Ulex gallii a
Galium saxatile o
Scabiosa succisa f
Senecio sylvaticus o
Leontodon hispidum f
" nudicaule o
Galeopsis tetrahit f

Juncus squarrosus o
Luzula multiflora f
,, var. congesta f
Agrostis tenuis f
Holcus lanatus f
Molinia cœrulea d
Blechnum spicant o
Lastrea aristata o
,, spinulosa o
Hypnum cupressiforme o
,, var. ericetorum f
Thuidium tamariscinum o
Laccaria laccata o

III. FORMATION AND PROBABLE HISTORY OF THE HEATH.

The heath is doubtless the surviving remnant of a much more extensive one and may be considered to represent a stage—exhibiting a number of successional phases—between a wet undrained peatmoss (Sphagnetum) and a dry heath. This view is substantiated by the marginal associations and the local history. The evidence scarcely indicates a degenerate forest though the alder thicket was probably more extensive and birches (Betula pubescens) more abundant. An oak-birch wood, in which Sphagnum is frequent, is present in the district, but does not immediately adjoin the heath. A road, which is known as the Drift, runs alongside the heath and this is locally supposed to have been cut as a drain. This supposition may be correct as the road, though very straight in comparison with the tortuous lanes usually found in country districts, cannot be definitely attributed to the Romans.

The two main factors determining the succession are (1) increased drainage leading to decreased moisture of the soil and (2) increased accumulation of humus on the hummocks isolated by by the drainage channels. At least five stages of succession may be distinguished in its present vegetation.

(1) Sphagnetum recurvii. Every portion of the heath has been more or less affected by human agencies but the lower, flatter and swampy portion has the nearest approximation to the primitive

condition, the flora being similar to that of peat mosses in other localities. This is the only area of Somerset in which Hypnum giganteum is known to occur; on the other hand the following plants which occur in similar associations in other parts of Somerset are not present or have not been noticed:—Peplis portula, Ranunculus flammula (a small form common in the bogs on the Quantocks), Wahlenbergia hederacea, Polytrichum commune, Hypnum fluitans. It is also to be noted that many of the plants found on the heath are now absent from the Somerset lowlands and are only found in such hilly regions as Exmoor and the Quantocks. Some bryophytes (Lepidozia setacea, Odontoschisma sphagni, Leptoscyphus anomalus, L. taylori) characteristic of peat mosses have not as yet been found in any part of Somerset. The wetter pockets of Sphagnum recurvum represent a more primitive condition of the heath than those of S. cymbifolium, the Sphagnetum cymbifolii being a later development.

- (2) Sphagnetum subnitentis. As the heath became drier Sphagnum subnitens became dominant. The Hypna and Sphagna which are now prevalent in the lower swampy portion and in the pockets became less abundant and gradually retreated to the wetter areas. A slight erosion of the humus from these areas and its retention and increase on the drained areas would then enable the next stage of succession to occur.
- (3) Molinietum. In many cases of progressive desiccation of a peat moss, the Sphagnetum does not directly give rise to a Molinietum but to an intermediate cotton-grass association (Briophoretum) occurs. There is no certain evidence of this succession stage occurring in this area. Eriophorum augustifolium is doubtfully recorded for the district in Murray's "Flora of Somerset," but though some parts of the heath seem to be suitable habitats, it has not been noticed either by myself or Rev. E. S. Marshall.

After the invasion of the *Molinia* the drainage areas became more constant and tussocks of this grass were formed. The increase in height of these tussocks has been chiefly due to the decay of the *Molinia* and *Myrica*. The furrows have been undoubtedly eroded but their ultimate increase in depth by such erosion is slight. During the wettest portion of the year (December is often the wettest month in this district) when erosion of an unprotected surface would be at a maximum, there is a superficial layer of dying vegetation, and the erosion does little more than compensate for the additional humus formed. *Nardus stricta* does not seem to

¹ W. G. Travis, "Plant Associations of some Lancashire Peat mosses."

have any successional relation to the Molinia, in fact it is usually found on the outer and wetter side of the tussocks, but this is probably owing to the rank growth of the Molinia towards the inside, and is an exception to the general relation of these plants.

- (4) The fourth successive stage is indicated by the central portions of the Molinia tussocks where Ulex gallii, Potentilla erecta, Holcus lanatus, etc., are frequent invaders. Calluna has not vet succeeded in obtaining a footing in these areas.
- (5) An extension of the fourth successive phase, or what may be considered as a fifth, is shown at the drier edges of the wet heath (see Fig. 1) where drainage takes place in three directions, as a ditch runs by the side of the road. Many of the plants common to the district occur here, a number of Rubus spp. (Rev. W. Moyle Rogers paid a lot of attention to this district), and also a number of hedgerow plants, but the succession has been very much modified by human agency. A much more natural succession is probably shown in the adjoining dry heath, the vegetational character of which is indicated by the following list of plants.

Polygala serpyllacea. Linum catharticum. Hypericum perforatum. humifusum.

Ulex europæns. " gallii. Vicia cracca. Potentilla erecta. Rubus fruticosus (agg.). Galium saxatile. Gnaphalium uliginosum. Senecio sylvaticus.

jacobæa. Hypochœris radicata. Leontodon hispidum. Teucrium scorodonia. Calluna vulgaris.

Juncus squarrosus. Holcus lanatus.

Anthoxanthum odoratum.

Deschampsia cæspitosa.

Agrostis tenuis. Pteris aquilina.

Lastrea aristata.

spinulosa. Blechnum spicant.

Hypnum cupressiforme

var. ericetorum.

Polytrichum juniperinum. Thuidium tamariscinum. Calypogeia trichomanis.

Lepiota procera. Boletus edulis.

The surrounding district has been largely reclaimed for pastureland and the survival of the wet heath is probably due to the fact that the Molinia and Myrica offer excellent cover for pheasants, the "spoor" of which is very plentiful. The heath has some local notoriety as the home of adders and countless midges, and the habits of these animals do not lessen the difficulties of examining its flora.

In conclusion I must tender my thanks to Mr. Tansley for his kind assistance in giving me valuable advice as to the methods of presenting the above account, and to Dr. Cavers for assistance in preparing the illustrations.

THE INTER-RELATIONSHIPS OF PROTISTA AND PRIMITIVE FUNGI.

By F. CAVERS.

I.—INTRODUCTION.

TN preparing the summarised compilation of literature on the primitive Algæ and on the Flagellata from which these have probably arisen, with an outline of the possible relationships between these organisms, which appeared in this journal some time ago (Cavers, 1913), it was at first intended to take a wider survey of the relations between the Protista and primitive algal and fungal forms as a whole. This would have been the more logical course, but it appeared better at that time to limit the scope of the compilation in order to deal more fully with the extensive additions made during recent years to our knowledge of the "algal" Flagellata and transitional forms, in particular those belonging to the Brown Series which have been so thoroughly worked out by Pascher, Scherffel and others whose labours have resulted in the discovery of many new forms, and may be said to have completely established the view that both Green and Brown Algæ are traceable by almost imperceptible gradations through an astonishing complete series of connecting forms to certain types of Flagellata from which they have probably originated.

As was pointed out in dealing with the "algal" series we are not justified in assuming that autotrophic pigmented organisms necessarily appeared in advance of, and gave rise to, forms devoid of light-absorbing pigments; indeed the argument, from general considerations, that organisms devoid of such definite cell-organs as chromatophores must have preceded in evolution those possessing them is strongly backed up by the knowledge that among the Bacteria we find many different processes of metabolism some of which cannot be confined within arbitrary definitions such as are implied by terms like "holophytic," "saprophytic," and so on, and that the conception of "prototrophic" may well be applied to those Bacteria which appear to have the power of fixing carbon dioxide as well as free nitrogen. Since the affinities of the Bacteria and of the Cyanophyceæ (Myxophyceæ) can hardly be said to have been cleared up to any appreciable extent by recent work, the former will be excluded from the present survey of the colourless organisms just as the latter were from that of the coloured organisms, though it may be remarked in passing that the Bacteria are in all probability a polyphyletic and unnatural group, for while some (the majority) of its members show fairly obvious affinities with the Flagellata others appear to approach in certain respects the Sarcodina among the Protozoa, and others again should probably be united with the higher Fungi. The curious and interesting group of Myxobacteriales is also excluded from the present review on the ground that there appears to be little or nothing to justify the view suggested by some writers that they are related to the Myxomycetes (Mycetozoa).

We are therefore mainly concerned here with the colourless non-autotrophic organisms comprised in the Flagellata, Protozoa,

Myxomycetes (in the wide sense) and Chytridiales. The working theory adopted as affording a plausible clue to the inter-relationships of these groups, or at any rate a thread upon which to hang the scattered facts here brought together, is that these forms have had a common origin in certain Flagellata which may with equally great or little plausibility be regarded also as the ancestors of the coloured or algal series which have already been dealt with. As was pointed out in considering these algal series, we find at the base of almost every line along the Green and Brown organisms a "mastigamæboid" form—a form with a naked pear-shaped body having at the pointed end one or more flagella while also capable of locomotion and holozoic ingestion by means of psuedopodia put out usually from the blunt posterior end; such forms are Chloramæba, Chrysamæba, Hymenomonas, Ochromonas and Wysotzkia. It was also pointed out that apart from their possession of chromatophores these forms show a striking resemblance to Mastigamæba and other colourless Flagellata usually placed in the groups Pantostomatineæ and Protomastigineæ—a resemblance which in the case of Chrysomonads especially extends to such details as the method of cystformation and which suggests the view that such Protomastiginean forms as Monas, Oikomonas, etc., may have been derived from Chrysomonads in the same way that such genera as Polytoma are regarded as colourless derivatives of Chlamydomonads, etc. This suggestion, followed out to its logical conclusion, involves the assumption that all the colourless Flagellata have arisen from coloured forms, an assumption which can only be justified if regarded as a purely speculative working theory. It was also suggested that these various mastigamæboid coloured forms, each apparently standing at the root of a remarkably complete ascending series of forms of which some at any rate lead definitely to algal types, might have arisen from a hypothetical Multicilia-like ancestor in which the spherical naked body possessed numerous uniformly distributed flagella and the power of putting out pseudopodia from any point as in Multicilia, but which differed from this colourless Flagellata genus in being an autotrophic form.

There appears to be a fairly general concensus of opinion among zoological writers that the Flagellata, and of these the group (Pantostomatineæ) which includes Multicilia and Mastigamæba and their allies, may be regarded as the most primitive group of Protozoa and as representing the common ancestors of all the classes of unicellular animals. Various recent botanical writers on the Myxomycetes (Mycetozoa) and allied groups such as certain Chytridiales, the Acrasieæ, etc., have referred—usually in a vague and general manner—to the possibility of relationships between these groups and certain groups of Protozoa, such as the Sarcodina, Heliozoa and Sporozoa; hence in this review these Protozoan groups will be considered in some detail in so far as their characters appear to throw light upon the relationships of the Myxomycetes, etc. As might be expected, it is the lower members of the various

II.—CLASSIFICATION OF THE PROTOZOA.

groups that are of interest in this connexion.

Four main groups of Protozoa are now generally recognised—Sarcodina, Flagellata, Sporozoa and Infusoria. The Sarcodina are

without a limiting cuticle, though frequently a test or shell is secreted, into which the protoplasm can be partly or entirely withdrawn; the adult has no specialised organs of locomotion-flagella or cilia-but moves and ingests food by more or less temporary extrusions of the protoplasm termed pseudopodia, i.e., in the manner called amœboid after the genus Amæba. The Flagellata (Mastigophora of many zoological writers) have in the adult or "vegetative" or trophic phase one or more special contractile protoplasmic outgrowths termed flagella which perform lashing whip-like movements; the protoplasm may be naked and amœboid, but more often is limited by a cuticle. The Sporozoa, which are internal parasites of higher animals, absorbing food from the internal juices of their hosts and never having in the vegetative or trophic phases any organs of locomotion or ingestion of food, are either naked and amæboid or covered by a cuticle; as the name implies, they reproduce typically by producing numerous small spores, though spore formation occurs also in other Protozoa. The Infusoria, which have been termed Heterokaryota from the fact that the nucleus is apparently always divided into two parts specialised in function and differing also in size (meganucleus and micronucleus), move and capture food (at least in the young state) by means of cilia-contractile filamentous protoplasmic outgrowths differing from flagella in their larger number and perhaps also in the mode of contraction and movement.

These four main groups have been variously combined into larger categories. For instance, Lankester (1885) divided the Protozoa into two main groups, the Gymnomyxa with naked protoplasm and indefinite form (Sarcodina), and the Corticata with the protoplasm limited by a firm membrane and hence with definite hody-form; but in the corticate groups there must be placed noncorticate amorphoid forms as Mastigamaba among the Flagellata or the malarial parasite among Sporozoa. Doflein (1911) made a twofold division into Ciliophora (Infusoria) with locomotion by cilia. and Plasmodroma with locomotion organs derived from protoplasmic processes, i.e., pseudopodia or flagella; but the distinction between flagella and cilia is not so sharp as to warrant such a division. Jackson (1888) suggested the union of the forms bearing flagella and cilia into one section, Plegepoda, and distinguished two other sections—Rhizopoda (Sarcodina), and Endoparasita (Sporozoa).

The classification of Protozoa is generally admitted to be a task of great difficulty. The Infusoria and the Sporozoa, though the majority of their members are clearly marked off-in the former case by the heterokaryote nuclear apparatus and the peculiar form of conjugation involving the reorganisation of this apparatus, in the latter by the possession of at least two alternating modes of broodformation, of which the first consists of aplanospores wherein is formed the second brood of sickle-shaped zoospores—cannot be sharply distinguished from other Protozoa when the lower forms of the two groups are taken into consideration; while the Sarcodina and the Flagellata are not only difficult to separate from each other but include in each case, particularly in the former, a number of forms which are very variously distributed by different writers among the generally recognised groups (Proteomyxa, Rhizopoda, etc., see below)—groups that can be kept apart only by arbitrary distinctions. Since the Flagellata are a generalised group and may be said to

constitute the Protista par excellence in the sense that they include forms combining the characters usually regarded as distinctive of plants and of animals, one might feel tempted to suggest their removal from the Protozoa but for the fact that they are separable from the Sarcodina by nothing more than the presence of a flagellum in the adult phase. For instance, Mastigamæba combines the characters of the Flagellata and of the Amæba-like Sarcodina in having an amœboid body which bears a flagellum, and it is placed in the Flagellata merely because the flagellum is retained throughout life instead of being present only in the young states as is the case in many of the Sarcodina. Bütschli regarded the Pantostomatineæ (the group including Mastigamæba and its allies) as representing the common ancestral type of the Protozoa, the flagellate young stages of many of the Sarcodina being considered as recapitulative larval stages. On this view the flagellum is regarded as a primitive organ, but a general objection similar to that raised in the case of the chromatophore arises here—it seems natural to suppose that flagellate organisms must have been preceded in evolution by others not possessing so definite an organ as the flagellum. However, this objection is to some extent weakened by the occurrence among various groups of what may fairly be regarded as transitional organs between flagella and pseudopodia, as well as between flagella and cilia. As pointed out by Minchin, more knowledge with regard to the nature and formation of the flagellum is needed in order to decide this point, and—since flagella are borne by many Bacteria which are on general grounds considered to be primitive organisms-particularly with regard to the question whether the flagella of Bacteria are of the same nature as those of Protozoa.

The Sarcodina, in the wide sense, are usually divided by zoological writers into six groups. The Mycetozoa (Myxomycetes) are distinguished by their tendency to the aggregation or fusion of the cells into more or less complex resting-groups or fructifications, and by their reproduction by flagellate or amœboid zoospores. The remaining groups, in which there is no such aggregation into plasmodia or fructifications, are separated chiefly by the characters of the pseudopodia. In Rhizopoda these are simple or if branched not coalescent, and are either blunt or if fine at the ends are dilated at the base. In Foraminifera they branch freely and coalesce to form networks. In the three other groups they are fine to the very base, are radially arranged, but rarely coalesce: in Heliozoa they have a central filament, in Radiolaria (body divided into a central and a peripheral part by a structure termed the central capsule) and in Proteomyxa (no central capsule) there is no central filament. No sharp lines can be drawn between these six groups: there are many genera which are by some systematists placed, for instance, in the division Filosa of the Rhizopoda, from their slender pseudopodia, and by others in the Foraminifera; while the division Proteomyxa is frankly admitted to be simply "a sort of lumber-room for forms which it is hard to place under Rhizopoda or Flagellata, and which produce simple cysts for reproduction, not fructifications like the Mycetozoa" (Hartog, 1909).

The Sporozoa, which are parasitic in higher animals, are usually intracellular for part at any rate of their life cycle, rarely possess pseudopodia or (except in the male gametes) flagella, and reproduce

by broad formation which is often of alternating types. The two most characteristic features of the Sporozoa are obviously correlated with their parasitic mode of life-they absorb fluid food osmotically and therefore lack organs for ingestion of solid food and they reproduce by the formation of minute germs, usually very numerous and often enclosed in firm protective envelopes, each with its contents constituting a spore. In most cases there is a second method of reproduction for increasing the number of the parasites in the individual host—this is distinguished as multiplicative or selfinfective or endogenous reproduction from the propagative or crossinfective or exogenous method (by means of resistant spores) which serves for infection of fresh hosts; and in most cases also sexual conjugation occurs at some period of the life cycle. The Sporozoa fall into two natural divisions, the Ectospora (Gregarinida, Coccidia, Hæmosporidia) in which the spore mother cells (sporoblasts) are formed at the periphery of the parent individual, and the Endospora (Myxosporidia, Actinomyxidia, Sarcosporidia, Haplosporidia. Exosporidia, Serosporidia) in which the spore mother cells arise in the interior of the body of the parent; that is, in the Ectospora sporulation is exogenous, in the Endospora it is endogenous. A further very general though not universal distinction between the two divisions is that in the Endospora sporulation goes on coincidently with vegetative (growth and trophic) life, while in the Ectospora it does not begin until the close of the vegetative or trophic period, i.e., until growth has ceased; on this account Schauding suggested for these divisions the terms Neosporidia and Telosporidia respectively. Moreover, a general distinction lies in the fact that the body in the Endospora is multinucleate but in the Ectospora uninucleate during the trophic period.

The Infusoria as defined by the dual nature of the nuclear apparatus—the meganucleus usually dividing by constriction and disappearing during conjugation, the micronucleus (sometimes multiple) dividing by mitosis and entering into conjugation and giving rise to the nuclei both large and small of the succeeding generation—fall into two divisions. The Ciliata, representing the highest type of Protozoa, have cilia or organs derived from cilia throughout life, are provided with a single permanent mouth (except in the parasitic Opalinopsidæ) flush with the body or at the base of an oral groove, and take in food by active swallowing or by ciliary action; while the Suctoria are rarely ciliated except in the young state and take in food by suction through protrusible hollow

tentacles.

III .- THE COLOURLESS FLAGELLATA.

From a general survey of the characters of the diversified forms of Protista classed by zoologists in the Protozoa it is fairly obvious that this heterogeneous group may for our present purpose be roughly divided into two main sections, one including a large proportion of generalised and relatively primitive forms, while the other comprises more complex and specialised forms. The generalised groups are the Flagellata and Sarcodina, among which there are forms which lead to the primitive Algæ, to the primitive Fungi and to the two specialised Protozoan groups—the Sporozoa and the Infusoria.

The general characters of the Flagellata as a class were treated in the earlier paper dealing with the coloured forms and their relationships to the primitive Algæ (Cavers, 1913, pp. 30-32), hence we need consider here in detail only the colourless Flagellate groups. These— apart from forms which are obviously colourless heterotrophic derivatives of coloured types classed with the Chrysomonads, etc.—belong to Senn's divisions Pantostomatineæ, Distomatineæ and Protomastigineæ. Specialised forms like the Cystoflagellata (Noctilucaceæ) and Hæmoflagellata (Trypanosomes) need not be dealt with, since we are concerned with those Protista which appear to be significant in connexion with the relationships

of the primitive Fungi.

Different writers have proposed various classifications of the colourless Flagellata, but in practically every recent system we find placed at the base of the series the group which Senn terms the Pantostomatineæ, and there is general agreement that the forms included here may be regarded as the most primitive types, from which the remaining Plagellata have probably arisen. Hartog (1909), after separating off the Dinoflagellata (Peridiniales) and in a later scheme (1910-11) also the Cystoflagellata (Noctilucaceæ), makes a primary division into Rhizoflagellata (Pantostomatineæ) and Euflagellata; the latter term is used by Willey and Hickson (1909) to include all the Flagellata except the Phytoflagellata (Volvocales), Dinoflagellata, Cystoflagellata and Silicoflagellata, but they also place Senn's Pantostomatineæ at the base of the Flagellata.

The Pantostomatineæ, or Rhizoflagellata, are characterised by the fact that solid food may be ingested at any point of the body in an amœboid fashion, i.e., by means of pseudopodia, the body being naked and the periplast represented only by an alveolar layer of protoplasm (Multicilia) or as ectoplasm covered by a very thin pellicle (Mastigamæba). They are divided into two families. In the Holomastigaceæ the body shows multilateral symmetry, being spherical with flagella scattered all over the surface, food is ingested by pseudopodia and also defæcated at all points, and locomotion is rotatory. This family includes the free-living genus Multicilia with one marine and one freshwater species, the latter (M. lacustris, Fig. 1, A) having numerous nuclei and differing in this respect from other Flagellata (excepting the Trypanosomes which are binucleate), and the closely related genus Grassia which occurs in the alimentary canal and blood of frogs; the only known method of reproduction is by median constriction and subsequent fission of the body.

The second family, the Rhizomastigaceæ, is larger and its members have only one or two flagella, but some of them are remarkably polymorphic in the sense that they may either live as free-swimming forms or may be amæboid or heliozooid (i.e., spherical with numerous fine radiating filamentous pseudopodia as in Heliozoa like Actinophrys); in the two latter conditions the body may be fixed to a substratum by a fine basal pseudopodial stalk, but in any case the flagella are retained through the amæboid or heliozooid phase.

According to Schuberg (Biol. Centralbl., Bd. 9 1909), however, the bodies occurring in the alimentary canal of frogs and described as *Grassia* by Fisch (Zeitschr. f. wiss. Zool., Bd. 42, 1885) are merely detached and deformed ciliated epithelium cells.

The Rhizomastigaceæ may be divided into uniflagellate and biflagellate genera, which present a parallel series. The uniflagellate forms include Mastigamæba, Mastigina, Mastigella, Actinomonas and Pteridomonas. In Mastigamæba (Fig. 1, B, C) the body is ovoid or elongated in the free-swimming phase, and even during this phase sometimes has pseudopodia, while in the amœboid phase it creeps by means of pseudopodia which are often branched; the flagellum, persistent through the amœboid phase, arises directly from the nucleus which lies at the anterior end of the body. The same relation between flagellum and nucleus, which apparently does not obtain in other Flagellata and which recalls the relation of the axial filament of the pseudopodia in Heliozoa to the nucleus, occurs in the allied genus Mastigina which differs from Mastigamæba in having the body covered by a thick pellicle. In these two genera the only form of reproduction known is by longitudinal fission in the motile state, but Goldschmidt (1907) has observed a sexual process in Mastigella (Fig. 1, D, E), which differs in having the flagellum quite independent of the nucleus and arising from a flagellar reservoir as in various other Plagellates. During the vegetative life of Mastigella vitrina binary fissions occur, preceded by withdrawal of the pseudopodia and flagellum and a mitotic division of the nucleus, the number of chromosomes seen in these divisions being about 40. Sexual reproduction is preceded by the formation of micro- and megagametocytes, in which minute granules of chromatin (chromidia) are extruded from the nucleus, increase in number and size, and form the nuclei of the gametes; in the formation of the megagametes at least one mitotic division occurs which is interpreted as a polar division, and a similar division probably occurs also in that of the microgametes, but the nuclear elements are so small that a definite reduction in number of chromosomes was not established. In both kinds of gametocytes encystment occurs, accompanied by withdrawal of pseudopodia and flagellum, but the microgametocyte encysts sooner than the megagametocyte; the gametes, both uniflagellate, escape from the gametocytes and conjugate to form an active zygote which divides several times by fission and then grows and assumes the usual characters of the genus. In Actinomonas (Fig. 1, F) the body is ovoid or spherical, capable only of slight changes in form, and gives out numerous fine radiating pseudopodia; it may either be free-swimming or become attached by a pseudopodium-like stalk at the posterior end. The pseudopodia are, as in Mastigella, provided with a central axis which springs from the endoplasm—this appears to be the case in all those Rhizomastigaceæ which have a heliozooid phase, or in which the pseudopodia become more or less permanent slender structures during part of the life of the organism—and in A. vernalis they are capable of being fully retracted. Pteridomonas (Fig. 1, G-I) is a remarkable genus, in which the single long stout flagellum is surrounded by a series of 8-12 short fine flagella, or cilia, which are capable of becoming rolled inwards like a watchspring and then bent outwards, exerting a jerking action by which the organism hops backwards; or these cilia may simply assist the flagellum in propelling the body forwards; while when the organism is attached by a stalk, formed as in Actinomonas, two of the cilia, somewhat thicker than the others, perform

movements which assist in bringing food particles near. Unfortunately nothing is known regarding the reproduction of Actinomonas and Pteridomonas.

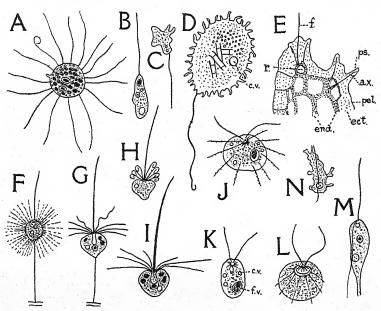


Fig. 1. Pantostomatineæ (Rhizoflagellata). A, Multicilia lacustris Lauterb. B, C, Mastigamæba invertens Klebs (B, free-swimming; C, creeping, with flagellum trailed behind). D, E, Mastigella vitrea Goldschm. (D, active individual, containing portions of filamentous algæ ingested as food; E, anterior end of body, showing axial strands from the endoplasm extending into the ectoplasm of the pseudopodia). F, Actinomonas mirabilis Kent, attached by pseudopodial stalk. G, H, I, Pteridomonas pulex Penard (G, attached; H, free-swimming with cilia retracted; I, free-swimming with cilia extended). J, K, L, Dimorpha mutans Gruber (J, individual with pseudopodia extended; K, with pseudopodia withdrawn; L, fixed and stained in heliozooid stage). M, N, Cercobodo longicauda Senn (M, free-swimming; N, amæboid stage). Lettering:—ax., axial strand; c.v., contractile vacuole; etc., ectoplasm; end., endoplasm; f., flagellum; f.v., food vacuole; pel., pellicle; ps., pseudopodium; r., flagellar reservoir.

The biflagellate genera of Rhizomastigaceæ are Cercobodo (Fig. 1, M, N) which is practically a biflagellate Mastigamæba and was named Dimastigamæba by Blochmann, and Dimorpha (Fig. 1, J—L) which corresponds to Actinomonas in the uniflagellate series but differs in not becoming attached by a pseudopodial stalk in the heliozooid stage. In this stage the fine granuliferous pseudopodia present a very striking resemblance to those of the Heliozoa, their axial filaments traversing both the cytoplasm and the nucleus and all diverging from a point in front of the latter whence also arise the two flagella. Even in the free-swimming phase, when the pseudopodia are withdrawn, these axial filaments persist (Fig. 1, L); food is ingested at any point by means of blunt "amæboid" pseudopodia.

The Pantostomatineæ may be regarded as the representatives of the generalised common stock from which the other Flagellata

have arisen, while from them lines may be traced which lead to the Proteomyxa, the Rhizopoda, the Foraminifera, the Heliozoa, and in fact to the whole of the remaining groups of Protozoa. The other colourless Flagellata are comprised in Senn's groups Protomastigineæ and Distomatineæ, which differ from the Pantostomatineæ in that ingestion is possible only at certain points of the body and which are easily derived from Pantostomatineæ along two diverging lines. The Distomatine are a small group, differing from all other Flagellata in having a bilateral but asymmetrical body with two mouth-spots (oral grooves) placed on two opposite surfaces and 4 to 8 flagella arranged in two groups in or close to the mouth-spots. The periplast is very thin and the body capable of some change of form, as is also the case in the large group Protomastigineæ which includes the great majority of the colourless Flagellata and is fairly sharply marked off from the Pantostomatineæ by having in the holozoic forms a single mouth-spot, usually anterior and terminal but in a few cases lateral, and from the Distomatineæ by never having the flagella in paired groups.

The Protomastigineæ are of great importance as including forms from which, according to the view usually taken, there may have arisen the coloured Flagellata groups—the Brown Flagellata (Chrysomonads in the wide sense, including Cryptomonads) and the Yellow-green Flagellata (Chloromonads in the wide sense, including Euglenineæ)—which have in turn given rise to the Brown and Yellow-green Algal series. The relationships of the transitional and algal members of these coloured series were discussed in the paper dealing with the Flagellata and Primitive Algæ. On the other hand, there are among the Protomastigineæ forms which may well serve as the starting-points of lines leading to the Chytridiales

and to the Myxomycetes, as well as to the Infusoria.

Senn divides the Protomastigineæ into nine families, each of which begins with a simple form essentially resembling a Pantostomatinean genus like Mastigamæba or Cercobodo in structure but showing an advance in organisation in some special feature which is further elaborated in the higher members of the family. According to the number and arrangement of the flagella five main groups can be distinguished, to which may be added the heterogeneous forms which in addition to 1 or 2 flagella have short cilium-like appendages and which probably form a transition to the Infusoria. Of these five larger groups the first, marked by the possession of a single flagellum, begins with Oikomonas (Fig. 2, A) which is practically a Mastigamæba with ingestion limited to a mouth-spot or "protrusible vacuole" at the base of the single anterior flagellum; this region thus forms a more or less permanent projecting organ of ingestion, though the vacuole subsequently migrates to the hinder part of the body, which is capable of amœboid movements and can also project to form an attaching stalk. A notable line arising from Oikomonas apparently leads through elongated spindle shaped forms like Leptomonas (parasitic) and Arcyromonas and flattened forms like Phyllomonas, the two latter with the flagellum directed backwards, to the parasitic Herpetomonas and the uniflagellate Trypanosomes (family Trypanomorphidæ, including Trypanomorpha) which have an undulating membrane and a dual nuclear apparatus. Two other lines, the interpretation of which appears to have led to some

confusion in the literature, are marked by the development of (1) a chitinous cup or theca within which the organism lives and (2) a protoplasmic collar-like outgrowth of the anterior end of the body. The first of these lines begins with Codonæca (Fig. 2, B), in which the organism is sessile in the cup, and probably leads through Bicaca (Fig. 2, C, D) in which there is a stalk, to the dendroid colonial genus Poteriodendron (Fig. 2, E). In these three genera the lip-like anterior projection foreshadowed in Oikomonas becomes more pronounced and the line marked by the possession of a welldeveloped plasmatic collar or peristome which is a modification of the ectoplasm of the anterior end of the body and which divides along with the latter, the plane of division being longitudinal as is usual in Flagellata though sometimes transverse; Codonosiga shows both longitudinal division involving the peristome (Fig. 2, F) and transverse division which occurs below the peristome, the lower half after division producing a new peristome of its own (Fig. 2, G). By the cohesion of the products of division in Codonosiga-like types there arise colonial forms such as Codonocladium (Fig. 2, H); while a further line begins with Salpingæca (Fig. 2, 1), combining the characters of Codonæca and Codosiga and having both theca and peristome, and leaning also to colonial forms, such as Polyaca (Fig. 2, J). A further choanoflagellate line begins with Diplosiga (Fig. 2, K) in which there are two concentric collars, and this line also leads to colonial forms.

The second main group of Protomastigineæ is biflagellate and isomastigote, being characterised by two flagella of equal length and both directed forwards. The simplest form, Amphimonas (Fig. 2, L), is practically a biflagellate Oikomonas, while Diplomita (Fig. 2, M) has a theca and corresponds to a biflagellate Codonaca or Dicaca; from both there arise branching colonial forms. In these forms (Amphimonadaceæ) as in Oikomonas, etc., food is ingested by an

anterior vacuole.

In the remaining Protomastigineæ with 2 or more flagella there is usually a marked difference in length or function or both between the flagella, often accompanied by specialisation of the cell in other respects. In the Monadaceæ (Paramastigoda) there is one long flagellum and one (rarely two) short accessory flagellum near its base; here also vacuolar ingestion takes place at the anterior end of the body. The Monadaceæ may be derived from the Amphimonads, or perhaps independently from a biflagellate Pantostomatinean like Cercobodo. In some species of Monas (Fig. 2, N) there are two short flagella; Physomonus (Fig. 2, O) shows a remarkable resemblance to Actinomonas, having numerous radiating thread-like pseudopodia; and there are branched colonial forms corresponding to those found in the uniflagellate families (Dendromonas, Anthophysa, etc.). Some of the simple Monadaceæ (Monas spp.) have an eye-spot and produce leucosin instead of the oil which is the characteristic product of the Plagellata, and in these respects as well as in the resemblance in general structure (apart from absence of chromatophores) and in mode of cyst formation they so closely approach the Ochromonads among the Chrysomonadineæ (see Cavers, 1913) that they may well be regarded as colourless forms derived from these brown Plagellates. Moreover, among the Chloromonads there are forms which strongly resemble

the Monadaceæ in general structure—for instance, Chloramæba is sometimes colourless and in this condition can hardly be distin-

guished from a Monas.

The Bodonaceæ, or Heteromastigoda, are closely related to the Monadaceæ, though they may have arisen directly from the Rhizomastigaceæ, for Bodo (Fig. 2, P) hardly differs from Cercobodo except that it does not pass into an amœboid phase—it ingests its food directly, in the amœboid manner, which is characteristic of the Bodonaceæ, the only member of this family showing vacuolar ingestion being Pleuromonas (Fig. 2, O); in both genera one of the flagella is frequently used to attach the organism to a firm substratum. In the remaining genera the body shows elaborations related to food ingestion; in Phyllomitus (Fig. 2, R) there is a funnel-like oral groove, in Colponema (Fig. 2, S) this groove is continued laterally to the posterior end of the body, and in Rhynchomonas (Fig. 2, T) one flagellum is replaced by a curious motile stout process forming a prolongation of the anterior end of the oral depression. It may be noted that the genera Bicaca and Poteriodendron are placed in this family by Lauterborn (1899) who regards the stalk by which the body in these thecate genera is attached to the base of the cup as being a second, backwardly directed, flagellum—an ingenious and highly probable interpretation; also that part of the Hæmoflagellata (Trypanosomes) is regarded as having arisen from Bodolike forms and as constituting a sub-family (Trypanosomatidæ) of Bodonaceæ, including the genera Trypanosoma, Trypanophis and Trypanoplasma.

The families Trimastigaceæ and Tetramitaceæ, characterised respectively by having three and four flagella inserted at the anterior pole of the body, despite certain general resemblances, are probably not closely related but have arisen independently from the Pantostomatinex, though they appear to have developed along parallel lines. Among Trimastigaceæ the body may be cylindrical with the flagella arising from the anterior pole (Elvirea, Fig. 2, U); or spindleshaped with one flagellum inserted at the anterior extremity and the other two at a constriction some distance behind this (Dallingeria, Fig. 2, V)—in these genera two flagella are directed backwards; or pyriform with a longitudinal wing-like projection. Similarly the Tetramitaceæ are divided into cylindrical forms either without (Trichomastix, Fig. 2, W) or more often with an oral groove which may be either limited to the anterior end of the body (Tetramitus, Fig. 2, X) or traverse its whole length (Collodictyon, Fig. 2, Y): and forms with a wing-like outgrowth or undulating membrane

(Trichomonas, Fig. 2, Z).

(To be continued).

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STRUCTURE AND DEVELOPMENT OF TARGIONIA HYPOPHYLLA.

By LILLIAN O'KEEFFE, B.Sc.

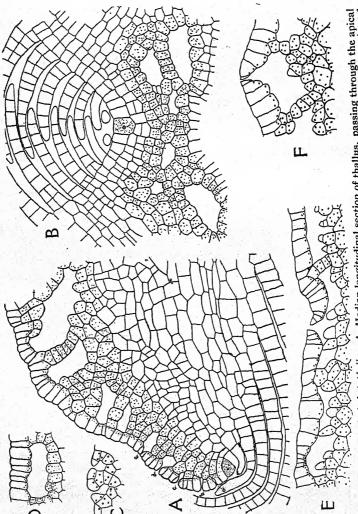
[WITH Two FIGURES IN THE TEXT.]

I. Introduction.

LTHOUGH a good deal has been published on the morphology of the interesting liverwort Targionia hypophylla, there are certain points which have not been covered in previous descriptions and others concerning which conflicting statements have been made by different investigators. The object of this paper is to give a brief statement of some of the results obtained in an examination of this plant. The material used was chiefly collected near Teignmouth, South Devon, by Dr. Cavers, who suggested the investigation and placed at my disposal not only a large supply of plants but also preparations made by himself when investigating the structure and biology of Targionia (3).

GROWING-POINT AND DEVELOPMENT OF AIR-CHAMBERS.

In his general account of the apical growth of the thallus in the Marchantiaceæ, Leitgeb (9, p. 2) simply states that in this group, as in the Ricciaceæ, growth is effected by a transverse row of initial cells, the number of these varying with the width of the groove in which the growing point is situated. The only accounts of apical growth in Targionia are those given by Cavers (3) and by Deutsch (6), the former writer stating that there is "a short transverse row of initial-cells lying almost in the plane of the ventral surface of the thallus," while Deutsch states that "the thallus is formed by the segmentation of a single, cuneate apical cell, cutting off segments on four faces" and that "relative to the apical cells found in the other genera of the Marchantiales, the apical cell of Targionia is rather small." It is obvious that the exact structure of the growing-point in a solid tissue can only be satisfactorily made out by the comparison of median longitudinal sections of the apex with sections made at right angles to these and to each other, so that the initial cell or cells may be viewed in longitudinal, horizontal and transverse section. It was found (both in my own sections and in re-examining those made by Dr. Cavers) that the account given by Deutsch is correct and that although in some cases two, and even three, cells of equal length and almost equal width were seen in horizontal and transverse sections through the growing-point, one of these cells—



the middle one when three equally long were present— was invariably wider than the others and was evidently the single apical cell, while the cells on either side were its youngest segments (Fig. 1, A, B).

According to Leitgeb the air-chambers in the thallus of the Marchantiales appear as depressions in the surface caused by definite points, typically situated where four superficial cells meet, lagging in growth and so becoming overgrown by the adjacent cells, the young chamber thus arising in the same manner as the pit in which the sexual organs (both kinds in Riccia, the antheridia in higher Marchantiales) become embedded, while the roofing-in of the chamber was attributed to the growth and division of the upper cells of the lamellæ thus formed. As shown by Barnes and Land (1), however, the chambers arise by the splitting apart of the superficial cells, in essentially the same way as the schizogenous intercellular Deutsch confirms this account for spaces in higher plants. Targionia, but states that while in the other Marchantiales described this splitting originates in an angle between the epidermal and hypodermal layers of cells, and proceeds outward toward the surface, in Targionia the process is reversed, the cracking apart starting at the surface between two epidermal cells and proceeding inward, subsequent divisions enlarging the space thus formed as well as the breadth of the roof.

The careful examination of sections taken in different planes shows that the chambers of Targionia arise in the way described briefly by Deutsch, but some interesting additional points were brought out. The first indications of the chambers were found at a very short distance behind the apical cell (Fig. 1, A), in which respect Targionia more closely resembles Riccia than the other Marchantiales figured by Barnes and Land, the first signs of splitting between the superficial cells being in fact detected in some cases only three cells behind the apex. The cleft begins at the surface but after it has proceeded inwards to about half the depth of the two cells (as seen in median longitudinal section of thallus) its progress seems to be arrested and a cavity is then formed by splitting of the walls between the epidermal and hypodermal cells (Fig. 1, A, a). From the regularity with which this appearance was presented in the early stages it was at first thought that the chambers in Targionia arose by the almost simultaneous occurrence of the two methods of cleavage (from without inwards and from within outwards) described respectively by Barnes and Land for various Marchantiales

and by Deutsch for Targionia. On plasmolysing hand-sections of fresh material, however, it was found that as the irrigating salt solution reached the section, the cells on shrinking, separated and a flask-like cavity was seen (Fig. 1, C); hence the crack between the cell-walls was evidently continuous, though owing to their turgescence the cells remained in contact at the middle. At a slightly later stage, a little further behind the apical cell, the young chamber is flask-like and open to the surface (Fig. 1, A, b, c), but it soon becomes closed again in the following manner. The epidermal cells grow unwards and towards each other, and each undergoes division by an oblique wall (Fig. 1, A, d), cutting off a cell which contributes to the formation of the dome-like roof of the chamber and these roofing cells come into contact so as to close the chamber (Fig. 1, A, e). That this closure is due to the turgor of these primary roof-cells is easily shown by plasmolysing fresh sections, when the roof-cells separate and the chamber becomes open again to the surface. This closed phase may last for a considerable time (Fig. 1, D, E). For instance, perfectly closed chambers were seen in which the diameter of the roof consisted of as many as twelve cells (as seen in median longitudinal section of thallus)—horizontal (surface) sections were, of course, also examined and showed the same.

The comparison of longitudinal and horizontal sections showed that the re-opening of the chamber takes place almost simultaneously with the earlier of the divisions which give rise to the concentric rings of cells which surround the pore, though in some cases the first of these divisions occurred while the pore was still closed. After a time, however, the pore becomes open, evidently owing to the lateral expansion of the chamber as the thallus grows in length and width, and the failure of the roof-cells to keep pace with this expansion. The innermost ring is, as stated by Deutsch, composed of dead cells, the contents of which become lost at a fairly early stage while the walls, especially on the free portion of the cell. become thickened and cutinised, this free portion growing inwards towards the centre of the pore and the cavity of the cell here becoming obliterated. The pore becomes widened with the surface growth of the thallus, and in the older parts of the thallus the pores gape widely and are elliptical in outline, as described by Miss Maybrook (10) in the case of Fegatella. The assimilating filaments, compact tissue and ventral scales have been sufficiently described by Cavers and no additional features of interest were observed in connexion with these.

III. ANTHERIDIAL RECEPTACLE.

As is well known, the antheridia of Targionia are produced on short ventro-lateral branches, arising in the same way as the vegetative adventitious branches which in this genus almost entirely replace the dichotomous apical branching usual in most other Marchantiales. My observations on the structure of the male branches entirely confirm the account given by Kashyan (7) for T. hypophylla var, integerrima, and some additional details were made out. As stated by Kashyap and by Cavers, every transition may be found, in examining a large amount of material, between the typical short stalked discoid male branches and ordinary "main" shoots bearing antheridia. The explanation is simply that the male branch may either have its growth arrested after producing a discoid antheridial cushion or may continue its growth and thus give rise to a "main" shoot which may branch apically or ventro-laterally or in both ways. Moreover, the growing apex in the former case may after a time cease to produce antheridia while continuing to grow, and in the latter case the branches formed may be sterile, in both cases leading to the formation of vegetative shoots.

A careful examination was made of the arrangement of the ventral scales on the male shoots, as well as of sections taken in several planes through these shoots, and this confirmed Kashyap's observation that the scales on these shoots are not arranged in two regular rows but are "scattered." In some cases, however, a definite arrangement in radiating rows could be made out both in the insertion of the scales and in the position and age of the antheridia themselves; that is, the youngest antheridia were found at several points on the periphery of the male "disc" or receptacle showing that the male receptacle of Targionia is essentially constructed on the same plan as that of Marchantia, though its margin is not lobed. A closer comparison may be made with the male receptacle of Fegatella, which as shown by Cavers (4) represents a branch system in which repeated dichotomy of the apex occurs but each growing point has a very short period of activity, so that while a distinctly centrifugal arrangement can be discerned in the antheridia the receptacle itself does not become lobed as in Marchantia where each growing-point continues to produce antheridia in acropetal succession for some time. These observations entirely confirm Kashyap's view that the male receptacle of Targionia represents a condensed branch system, the non-commital term "condensed" being perhaps preferable to the term "reduced"

which implies phylogenetic reduction from a type like Marchantia, while as we have seen every transition may be found in Targionia between condensed male shoots of limited growth and well-developed ordinary thalli bearing antheridia.

IV. ARCHEGONIAL RECEPTACLE.

The development of the archegonial receptacle and of the involucre has been described by Leitgeb (9), Campbell (2) and Deutsch (6), the last writer introducing the useful term "fruiting surface" for the surface or pad on which the archegonia are borne terminally on the thallus. This surface, on which the archegonia, usually about 7 but up to 9 or 10 in number in some cases, are developed in acropetal order in a zigzag row, slopes forward and downward; the apical cell is clearly seen in front of the youngest archegonium, and since each of its dorsal segments produces an archegonium, these organs are at first closely crowded, very little vegetative tissue being formed in the upper part of the thallus in this region. The result is that the archegonial surface comes to lie in a shallow depression, the lower (anterior) margin of which is occupied by the apical cell—the time at which this cell ceases to function appears to be, like the number of archegonia produced, conditioned by the occurrence of fertilisation in one or more of the archegonia. As Deutsch points out, the development of the involucre is closely bound up with that of the archegonial or fruiting surface, and it may in fact be considered as simply representing the lateral or peripheral region of this surface, the earliest stages in its development synchronising with the appearance of the first archegonia, and consisting simply in the forward growth of the tissue around the archegonial depression to form two curved lateral ridges. These ridges at first consist of compact tissue, but at a later stage air-chambers are developed, especially in the upper portion of each ridge, so that when mature the involucre, the two valves of which have been formed by the continued growth of the ridges, appears in vertical transverse sections as a continuation of the ordinary thallus tissue, each valve having air-chambers in its upper portion.

As the valves of the involucre grow forward they curve inwards towards the middle line of the archegonial surface, keeping pace with the growth in length of the archegonia, and their free edges come close together so that the opening to the archegonial depression becomes narrowed and slit-like. Deutsch reports a case in which the involucre was "complete and well developed while the eggs of

Structure & Development of Targionia hypophylla. 111

the archegonia it surrounded were still unfertilised," but in my preparations it was found that the *completion* of the involucre—i.e., its closure, the development of the interlocking marginal teeth, and the other processes described below—never took place unless one or more of the archegonia had been fertilised and showed the early stages of embryogeny. Hence the development of the involucre

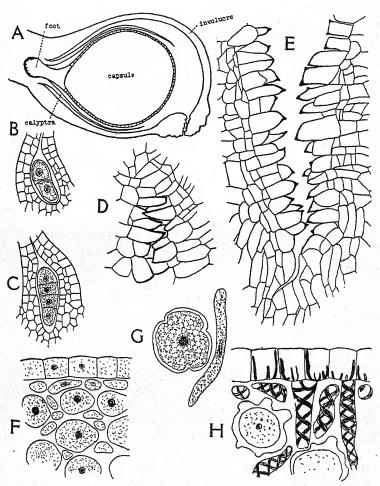


FIG. 2. Targionia hypophylla. A. Median longitudinal section of plant with nearly mature sporogonium. B, C. Early stages in development of sporogonium, in longitudinal section. D. Part of suture of involucre, showing the interlocking tooth-like cells on the margins of the valves. E. Part of involucre caused to gape by pressure, showing the interlocking marginal cells. F. Part of section of capsule, soon after the rounding off of the spore mothercells, between which are the sterile (elater-forming) cells. G. Spore-mothercell and young elater. H. Part of section of capsule showing two fixed elaters.

may be divided into two stages separated by the occurrence of fertilisation, which appears to be essential for the beginning of the second stage. In the first stage the involucre reaches the condition just described-i.e., it consists of two crescentic ridges which together with the archegonial depression form an ovoid cavity having its longer axis in the median line of the thallus and having the margins separated by a gap (through which enter the antherozoids), and it projects very slightly from the general surface of the After fertilisation has taken place, the two valves or ridges undergo active growth, the cavity being greatly enlarged; the margins come together and the walls of the cells in this region become thickened, cutinised and coloured reddish or violet (the same changes taking place over the outer surface of the valves), the cells at the margins become tooth-like and form interlocking processes which cause the complete closure of the involucre (Fig. 2, A, D). The suture thus formed is easily separated by pressure on the involucre, which can thus be made to gape widely open (Fig. 2, E), so that there is no fusion of the marginal cells, merely an interdigitation of the tooth-like processes.

V. Sporogonium.

The early stages in development of the sporogonium were followed in some detail, and were found to differ somewhat from what has generally been described as the typical embryogeny of Marchantiales, namely, the early formation of an octant stage. No such stage was observed, all the young embryos seen consisting of a single row of as many as five cells, but more often either three or four (Fig. 2, B, C), before any longitudinal divisions had taken This "filamentous" type of embryo has generally been regarded as typical for the Jungermanniales, as opposed to the early octant formation characteristic of Marchantiales, but Meyer (11) has recently described a similar cell-row in the early embryogeny of Plagiochasma, his figures closely agreeing with the series observed by me in Targionia. Since only one sporogonium is formed in each involucre, i.e., on each shoot, it is less easy to obtain a complete series of stages in Targionia than in the higher Marchantiales where each archegoniophore produces a number of sporogonia, but a fairly good consecutive series was obtained showing all the chief stages from fertilised egg to nearly mature sporogonium. The differentiation of the one-layered capsule wall from the central fertile tissue takes place at a fairly early stage, the periclinal

divisions which separate off the primary wall layer usually following immediately upon the first longitudinal divisions in the young embryo, which divisions take place at right angles so that the upper part of the embryo consists of a series of cruciform tiers of four cells each. For some time the embryo is pear-shaped, with the upper (capsule) end broader than the lower (foot) end, but this stage is of short duration and soon passes over into a longerenduring dumb-bell stage in which the capsule is spherical and is separated from the club-shaped and bluntly pointed foot by the (at this stage relatively thick) neck or seta portion. During this dumbbell phase divisions occur vigorously both in the capsule and foot, but especially in the internal (sporogenous) tissue of the former, and the foot at a relatively early stage attains practically its full size while the capsule continues to grow and becomes eventually very much larger, its diameter when nearly mature being about ten times that of the foot. The surface cells of the foot project as short papillæ or haustoria, these cells and also those of the immediately surrounding tissue of the thallus and base of the calvptra staining deeply. That the growing foot exerts considerable pressure on the tissue in contact with it is seen from the small size of the cells outside of the foot, but the appearance of these deeply-staining small cells shows also that active divisions occur in this adjacent tissue, so that the smallness of the cells is not due merely to the pressure of the foot. The space between the foot and the tissue of the calyptra and thallus contains deeply-staining mucilage, which is also seen in much earlier stages and even around the egg itself when the latter becomes rounded off prior to fertilisation.

The differentiation of the central tissue of the capsule into spore-mother-cells and elaters takes place at a relatively late stage, and the two kinds of cells are very irregularly arranged, not forming rows as in Fegatella, Monoclea, Marchantia, etc. The fertile cells become distinguished by continuing to grow in diameter and retaining their deeply stainable character, while the sterile cells mingled irregularly with them remain small and are less deeply stained, but they do not grow appreciably in length until the spore-mother-cells begin to round off. The spore-mother-cells are described by Deutsch as being spherical, as is usual in the Marchantiales, but in sections as well as in teased out material from developing capsules these cells were seen to be slightly four-lobed prior to the division of the nucleus (Fig. 2, G), as described by Cavers (3) and Leclerc du

Sablon (8) and figured by the latter writer. The lobing was in many cases very slight indeed, and cannot be described as similar to the deep lobing characteristic of the spore-mother-cells of the Jungermanniales.

Many of the sterile cells (elaters) are seen to lie immediately within the single-layered capsule wall, in some cases forming a more or less definite layer in this region of the young capsule (Fig. 2, F). As stated by Kashyap (7), some of the elaters are in most cases found attached to both the upper and lower portions of the capsule (Fig. 2, H), though the number of these attached elaters is relatively small and their distribution (apart from the "polarity" they show in occurring at the two opposite ends of the long axis of the capsule) irregular. In a few of the capsules sectioned very few, and occasionally none, of these fixed elaters could be found; the statement by Deutsch that none occur may perhaps be attributed to his having examined few capsules. In some places the sterile cells immediately within the capsule wall fail to separate from this at any point and consequently remain attached so that at such points the wall appears two-layered, but in most cases the separation is effected at an early stage, and when the developing elater fails to split completely from the wall-layer the attachment persists so that the mature capsule usually contains a number of these "fixed elaters."

VI. SUMMARY.

1. The thallus of Targionia hypophylla grows by means of a single apical cell, from which segments are cut off dorsally, ventrally and on either side. The air-chambers arise by splitting between the epidermal cells, the split extending from the surface inwards through the entire depth of the epidermis; this process is followed by partial closure of the crack due to turgor of the bounding cells; the young chamber next undergoes extension owing to general growth of the thallus tissue, but remains closed for a considerable time until the divisions occur which cut out the concentric cell-rings around the pore, when the latter opens and continues gradually to increase in area until the general growth of the thallus ceases. The membrane-like rim around the pore of the chamber is formed from the innermost ring of surrounding cells, the cavity of these cells being almost obliterated by thickening of the walls.

2. The antheridial receptacle may be developed on special short stalked disc-like branches of limited growth or on ordinary thallus branches, every intermediate condition being found between

the two extremes. The centrifugal arrangement of the antheridia and the scattered distribution of the ventral scales on the disc-like receptacle indicate that the latter represents a condensed branch system in which dichotomy occurs rapidly and the several growing-points formed are of short-lived activity.

- 3. The bivalved involucre develops simultaneously with the archegonial group and represents the peripheral region of the archegonial surface, but its further growth, the formation of interlocking processes on its margin, and its closure until the extrusion of the capsule are dependent on the occurrence of fertilisation in one or more of the archegonia.
- 4. The young sporogonium does not show the octant stage usually regarded as characteristic of Marchantiales, but approaches the "Jungermannia type," a row of cells being formed by successive transverse divsions before the first longitudinal divisions occur. The spore-mother-cells and the elaters occur in approximately equal numbers and are irregularly mingled, but there is invariably a layer of elater-forming cells immediately within the single-layered capsule-wall and these cells may either remain attached by their entire length to the inside of the capsule-wall, or by one end only, in the former case making the wall two-layered in places, in the latter case forming fixed elaters.

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FURTHER OBSERVATIONS ON THE HEATH ASSOCIATION ON HINDHEAD COMMON.

By F. E. Fritsch, D.Sc., Ph.D., and E. J. Salisbury, D.Sc.
[With Plate I and One Figure in the text].

THE present paper is a continuation of observations on the heath association on Hindhead Common made by staff and students of the Botanical Department, East London College and, in order to facilitate comprehension of the subsequent matter, a brief recapitulation of the main topographical features may first be given (see 3). The main area consists of a "central ridge" gradually sloping down from the north-east and bounded by two converging valleys (A and B in Fig. 1) meeting at the south-western end. From this point the valley A runs onward in a south-westerly direction gradually passing over into that leading down to Shottermill, so that the main valley-system is more or less in the form of a Y; from the main stem of the Y two further south-easterly valleys (C and D) arise, approximately at distances of 330 and 730 yards respectively from the point of junction of A and B. The tops of the ridges are mainly occupied by tall Calluna and Ulex nanus (CU facies), whilst the slopes, which appear to have been subject to more recent fires. bear a mixed vegetation composed chiefly of low Calluna, Ulex nanus and Erica cinerea (CUE facies).

As we are largely concerned with colonisation and rejuvenation (i.e., sprouting of stools after a fire) on the different burnt areas, their distribution may be enumerated. In this connection we shall represent each by the symbol F, followed by a numeral indicating

- F 1. Burnt June 1913; situated on slope in valley D; aspect S.W.
- F 2. Burnt in April, 1912; situated on slope in valley C: aspect S.W.

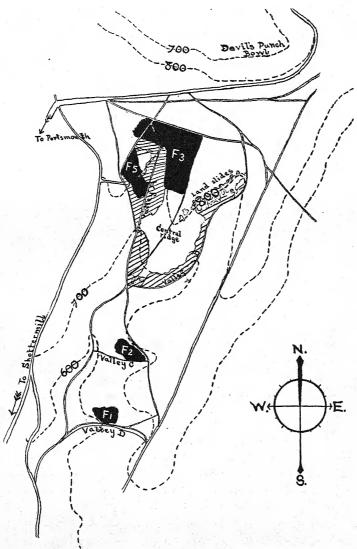


Fig. 1. Map of Hindhead Common. For further explanation see Text.

- F 3. Burnt August, 1911; situated on both sides of valley A, on slopes and central ridge; aspects respectively W.N.W. and E.S.E.
- F 5. Burnt 1909; situated mainly on N.W. slope of valley A; aspect E.S.E.
- F 7. Probably burnt in 1907, but exact date of fire unknown; developed as CUE facies on lower slopes of "central ridge" (shaded in map); aspects diverse.

The subsequent matter is divided into the following sections:-

- A. The primary effects of burning (p. 118). (1) Destruction of the aerial organs (p. 118). (2) Killing of certain constituents of the vegetation (p. 119). (3) Destruction of the peat (p. 121).
- B. The effects of exposure (p. 122). (1) Evaporation-data (p. 122). (2) Wind-trimming (p. 125). (3) Growth-forms on the land-slides (p. 128).
- C. Colonisation (p. 129). (1) Cryptogamic succession (p. 129). (2) Phanerogamic succession (p. 132).

We take this opportunity of expressing our indebtedness to the Local Committee of the National Trust, in charge of the Hindhead Common, for giving us facilities to carry on the work, and particularly to Mr. W. C. Marshall and Mr. H. B. Dempsey for useful local information. We have also to acknowledge a grant from the Council of the East London College in aid of expenses incurred in connection with the work.

A .- THE PRIMARY EFFECTS OF BURNING.

The first results of a heath-fire may be considered under three headings, viz., (1) the destruction of the aerial organs, (2) the killing of certain constituents of the vegetation, and (3) partial or complete incineration of the peat.

(1) Destruction of the aerial organs.

At the outset attention may be called to the eccentricities which heath-fires often exhibit. Small patches of the vegetation are frequently left untouched, whilst all around is burnt. The limits of a fire are also extremely arbitrary. The most striking case of this kind is that furnished by the fire which took place some seven years ago and which left the whole of the "central ridge" untouched (3, p. 153), the edge of the fire being now marked by a sudden drop in the level of the vegetation, as we pass from the unburnt (15 years

old) to the burnt area (about 7 years old). It may be well to mention that, since the first account of the Hindhead Heath was published, we have collected local information as to the actual occurrence of such a fire leaving the "central ridge" untouched. The fact that later fires (e.g., F 3) may sweep across such lines of demarcation of former fires would appear to indicate that direction of the wind is a prime cause in their formation.

As a natural consequence of the firing of the vegetation, the mutual shelter afforded by Calluna, Erica, etc., is removed, so that the new growth suffers from the full rigours of exposure. At the same time the inhibiting effect, upon other plants, of the shade cast by tall Calluna (6, p. 104) ceases; as a consequence, invasion by light-loving species becomes possible. Hence we find that, whilst growth of the shrubby members is slow on a recently burnt area, the primary flora exhibits much greater diversity than in subsequent phases.

(2) Killing of certain constituents of the vegetation.

Although the heat generated by a heath-fire is very considerable, it is not sufficient to destroy all the members of the heath-flora, and indeed its effects in this respect are selective. Thus, Ulex europæus, U. nanus, Vaccinium myrtillus, Erica tetralix, Pteris aquilina, Molinia cærulea, and all the trees, commonly rejuvenate from old stools after burning. In the case of Erica cinerea this would appear to be more rare, whilst sprouting stools of Calluna are few and far between. On a given area it was found that all the Callunas (54) were dead, whilst of the 57 Ulex nanus plants over 87% had survived. Sprouting Carex pilulifera is but seldom found, which is in conformity with its sparse occurrence in the closed heath-association. These facts are illustrated by the following table showing the number of sprouting stools of four different species on a given area.

TABLE I.

	U^{i}	lex nanus	. Eri	ca cine	rea.	Vaccini	um. ¹	Callur	ıa.
Area F 2	•••	974	• • • •	91	•••	14	•••	3	
Area F3		160	***	69	• • • •			-	

It was previously suggested (3, p. 159) that the selective killing basic might be related to the rooting depths of the forms concerned, but this view has not been supported by subsequent observation. Thus, a number of tall Calluna specimens were found to have roots

 $^{^{\}mbox{\scriptsize 1}}$ Vaccinium was very sparsely scattered on the first, and absent from the second, of these areas.

penetrating to an average depth of over nine inches, whereas in the case of *Erica tetralix*, which as already stated almost invariably rejuvenates, the average depth is under six inches; and the same is true for *Molinia* and *Carex pilulifera*, whose average rooting depth is about three inches. It is, nevertheless, a fact that *Ulex nanus*, which so commonly survives, has deeper roots than any of the Ericaceous forms, whilst *Erica cinerea*, which is frequently destroyed, has relatively shallow roots (see Table II).

TABLE II.

Rooting depths (in inches) of plants on the Hindhead heath.

(Heights of aerial organs in brackets).

Calluna:— 18 (35); 10 (32); 8 (32); 6.5 (26); 6 (24); 6 (18).

Erica cinerea: — 9.5 (8); 6 (30); 3 (20.5); 3 (16).

Erica tetralix: -6.5 (11); 4.5 (9).

Ulex nanus :- 24 (24); 12 (32).

A careful examination of dead and rejuvenating stools discloses the fact that the latter fall into two categories, viz., (a) those in which the branching of the crown takes place beneath, or in close contact with, the general surface of the soil, and (b) those in which branching, although occurring above the surface, is so profuse as rapidly to accumulate a mound-like protective covering of humus. In the case of Ulex nanus the former condition generally obtains. and it appears that such few specimens as are killed have a relatively exposed crown. This point seems to be the determining factor as to whether a Calluna sprouts or not; thus all sprouting specimens of this plant examined proved to have a crown that was more or less completely buried, whilst the numerous dead specimens were found to have branched above the surface of the soil (Plate I. Phots. 3, 4). The same features were observed in Erica cinerea, but. since a large percentage of plants of this species have buried crowns. the proportion of survivors is greater.

Erica tetralix affords an example of the second category. Here numerous branches arise just above the surface of the ground forming a trap for humus, so that after a few years they are embedded. The efficiency of this covering is demonstrated by the apparent absence of non-rejuvenating E. tetralix. Tussock-forms, like Molinia cœrulea and Carex pilulifera, probably owe their immunity to the same feature.

The cause of survival in the case of Vaccinium and Pteris is slightly different, for here the perennating rhizomes are situated

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underground at average depths of about one and three inches respectively.

We have already called attention to the removal of shelter by burning, resulting in a corresponding increase in evaporation from the soil, and this is probably enhanced by the hard surface-crust left after a fire. Moreover, the water-capacity of the soil is reduced owing to the destruction of the peat (cf. p. 122). Forms which root deeply will consequently be in a more advantageous condition as regards their water supply, until shelter is re-established, than shallow-rooting forms. This may in part account for the fact that *U. nanus* begins to sprout almost immediately, whilst in the case of *Calluna, Erica*, etc., there is considerable delay, often amounting to as much as a year.

Observations made on an area burnt in June (P 1) i.e., in the middle of the growing season, showed that about half the U. nanus sprouted in the same season, whilst the remainder were delayed until the subsequent April. On the other hand, in the case of a fire which took place later in the year, viz., in August (F 3), all the Ulex sprouted simultaneously in the following season. This may imply that if a fire destroys the U. nanus in the middle of its growing period, the plants receive such a set-back that many are unable to rejuvenate immediately. There are some indications that other plants may be similarly influenced in their rejuvenation by the time of the year at which the fire occurs. We have, unfortunately, not been present at any of the fires on the Hindhead Common, so that we know nothing of the conditions of burning. Elgee (2, p. 8), however, has pointed out in this connection that "where the fire passes over the heather with the wind behind it, the plants come again much earlier than when the burning has been against the wind and so more thorough."

(3) Destruction of the peat.

It is to be noted that the peat on the oldest part of the heath (i.e. the north-western slopes of the central ridge) reaches a depth of from 3-5 inches, and here the Calluna and Vaccinium attain their maximum development. On the other hand, on all areas recently burnt, there is little or no peat, its place being taken by the charred crust already referred to. The destruction of the peat may well account for the poor growth of Calluna in the first years following a fire, and also for the predominance of Erica cinerea in the early phases, since the latter is favoured by a dry soil (7, pp. 104, 109).

It is striking that the *Vaccium* over most of the Hindhead heath is of very low growth, and this is probably to be related to the frequent fires which prevent any considerable accumulation of peat.

Estimations of the humus-content have not been made on a sufficient scale to draw exact inferences as to the amount of organic matter in successive years after a fire. It is clear, however, that at first the humus-content is small (on an average 7.3% of the dry weight) and there does not seem to be any rapid increase until several years have elapsed. On the other hand, in the oldest parts of the heath (CU) the humus-content is from two to three times as great, reaching a maximum of about 30% where Vaccinium is dominant. The regions with poor Calluna (p. 132) have a relatively low humus-content, and it is significant in this connection that the amount of organic matter on the slopes of recently burnt areas is lower than on the level.

As a result of the increase of humus there is a marked increase of water-content; thus after a week's heavy rain it was found that, whereas on burnt areas the water-content was 11-19% of the dry weight, in the tall *Calluna* it was 31-39%, and where *Vaccinium* becomes dominant nearly 70%.

B.—THE EFFECTS OF EXPOSURE.

(1) Evaporation-data.

Attention has often been called to the uniform level of the vegetation of heaths, a feature which is exhibited in a more or less marked degree during every phase of its development (cf. p. 129 et seq.), but most pronouncedly in the final stage which we have termed tall Calluna (CU facies). This is due to the dying away of most of the projecting tips which, owing to their isolation, are subjected to extreme exposure (3, p. 153). A measure of the extent to which mutual shelter is afforded by the vegetation, when growing up en masse, is furnished by estimations of the difference in the rate of evaporation as computed at succesive levels above the soil-surface.

All our evaporation-data have been obtained in the following way. A number of porous pots of about 60 cc. capacity were filled with boiled water to a known level; their open ends were plugged with corks, previously impregnated with paraffin-wax and pierced by a short length of glass tubing whose outer end was sharply bent downwards as a fine capillary tube. The pots were fixed in vertical series to upright posts by means of wire attachments. The drop in level of the contained water was estimated at frequent intervals, the water being at the same time restored to its original level.

TABLE III.

Evaporation (in Cubic Centimetres) in Tall Calluna (CU Facies).

			GROU	ND LEVEL		T BELOW		JUST ABOVE TOP
					OF	VEGETATIO	ои.	OF VEGETATION.
Series	1	(av. daily av. tota	·	·67	•••	2.48	•••	2.96
		-			•••	1.69	•••	1.94
Series	9	Jav. daily		1.13	•••	2.57	• • •	3.29
		•			•••	1.65	•••	2.26
Series	3	Jav. daily	<i></i>	1.25	•••	2.69	• • •	4.33
Geries	Ü	(av. total	,	1.16	• • •	1.82	•••	2.58
Series	1	Sav. daily av. total		1.02	•••	2.44	•••	4.61
		•			•••	1.50	•••	2.98
Series	5	{av. daily {av. tota		1.36	• • •	2.33		2.89
Octios	Ü	av. tota	٠	·86	•••	1.33	•••	1.75
Series	В	jav. daily av. tota	<i></i>	1.19		2.36	•••	4.18
Gerica	٠	av. tota	l	·58	•••	1.24	•••	1.55
		laily evap for al	1					
the	ser	ries	•••	1.10	•••	2.48	•••	3.71

TABLE IV.

Evaporation (in Cubic Centimetres) in Low Calluna (CUE Facies).

		GROUND LEVEL.		JUST ABO	VE TOP OF VEGETA	TION.
Series	1 {av. daily av. total	1·59 1 1·16	•••	• • • •	2·32 2·12	
Series	2 \{av. daily av. total	7 1·34 1 ·98	•••	•••	3·44 2·84	
Series	3 av. daily	7 1·68 1 1·20			3·65 2·37	
	4 av. daily		•••		2·98 2·02	
Averag	e daily, for eries	1.47		•••	3·10	

From Tables III and IV it is apparent that the evaporation above the general vegetation-level is from two to three times greater than on the ground, and in the case of tall Calluna the evaporation just above the vegetation-level is about half as much again as just below. Moreover it is to be noted that the difference between evaporation on the ground and just above the vegetation-level is, during the day, considerably greater on the ridge (tall-Calluna) than in the valleys (CUE facies). This is in conformity with the greater persistence of solitary projecting shoots in the valleys and on the lower parts of the slopes as compared with the higher levels.

Attention may be drawn to the fact that series 2, 4 and 6 in Table III were obtained amongst some of the tallest heather on the area and that these exhibit a much more pronounced difference between the average daily and the average total evaporation at the ground-level than the series 1, 3 and 5 and those in Table IV. As a matter of fact the evaporation at night on the ground, in Calluna over three feet high, is only about one-third of that in the CUE facies where the Calluna is about one foot high (see also Table V). This shows that the soil of the former is subjected to considerably less desiccation.

Evaporation is, however, a much more potent factor after all shelter has been removed by fire, as shown in Table V. From this it is apparent that evaporation at the ground-level is more than doubled after burning (cf. Table III). In Table V, the first two series of readings were taken on hot sunny days, whereas series 3-5 were obtained on dull windy days. It will be noted that in the former set of readings the evaporation at the 3 ft. level is lower than at 18 ins., a feature which is not apparent in the latter. Moreover, in all the series, night readings in general show little difference as between the 18 in. and the 3 ft. levels. These results point to radiation from the bare ground being an important factor at levels not far above the surface.

TABLE V.

Evaporation (in Cubic Centimetres) on Burnt Areas.

	GROUND.		18 INS.		3 FT.
Series 7 Sav. da	ily 3.69		4·2I	•••	3.34
(F 3 on slope) (av. tot	al 3.27		3.45		3.37
Series 2 (F 3 near top av. da av. tot of slope)	•	•••	3·97 3·26		3·04 2·67
Series 3 (F 2 top of av. dayslope)		•••	2·42 1·68	•••	2·91 2·08
Series 4 (F 2 half way av. da av. tot down slope)		•••	2·88 2·10		3·02 2·17
Series 5 (F 2 base of { av. da av. to slope)			2·65 1·90		2·92 2·11
Average daily for series	all 2·56		3.22		3.05

On the bare areas caused by landslides (3, p. 161) we have extreme exposure as a permanent condition, the average daily evaporation at the ground-level being 2·12 cc. and at the 3 ft. level 3 cc. In comparing these figures with those from the burnt stretches it must be borne in mind that the areas under consideration are situated in the trough formed by valley B.

Temperature-readings have shown that on sunny days the bare surfaces become heated to such an extent that just after midday the temperature of the top-crust is, on the average, about 2° C. above that of the air, whereas in the closed association it is approximately $4\cdot5^{\circ}$ C. below or, where provided with a covering of moss as much as $5\cdot5^{\circ}$ C. below. The great heating of the soil on exposed areas will naturally lead to much greater loss of water than in the closed association, so that even if the soil had the same water-capacity and were sheltered, it would necessarily be drier on the exposed area.

(2) Wind-trimming.

The wind-trimming in the case of Calluna to which we have already referred bears testimony to the adverse conditions at some height from the ground. The same phenomenon can be observed in all the true heath-representatives wherever they are subjected to such exposure.

The most general type of growth-form resulting from exposure is that seen on the burnt areas, particularly in the case of Ulex nanus in which the uprising branches are relatively short and closely aggregated together, extension being mainly in the horizontal direction. The whole therefore forms a slightly convex cushion or hummock. Young plants of most of the shrubby species in the more exposed situations almost invariably exhibit a prostrate habit, due to the relative unimportance of the main axis (which in the case of U. nanus generally dies away) and the development of numerous laterals in close contact with the surface. It has been observed that seedlings of U. nanus growing in hollows of burnt areas sometimes exhibit a vertical development of the main axis until the level of the surrounding soil is reached, whereupon growth of the main axis is arrested and horizontal laterals are produced. The prostrate type, although particularly characteristic of burnt areas, is often retained to a more or less marked extent, on the upper slopes, even in the closed association.

In a later stage of development one or more of the branches of the cushions grow in a vertical direction, so that the flattened character is obscured. This is probably correlated with the establishment of a root-system adequate to cope with the resulting increase of transpiration. That the prostrate habit, at first assumed, is due to exposure is shown by a comparison of the relative frequency, in situations of varying exposure, of plants (a) with all their branches prostrate, and (b) with one or more of their branches ascending (see Table VI). Such a comparison brings out the facts that (1) the percentage of prostrate plants is much greater in the more exposed situations, and (2) the number of specimens retaining the prostrate habit becomes smaller, the longer the interval that has elapsed since a fire, and consequently the greater the density of the vegetation.

TABLE VI.

Percentages of Completely Prostrate Specimens of ULEX NANUS ON BURNT AREAS.

DIRECTION OF PREVAILING WINDS, S.W.

	LOCALITY.	EXTREME EXPO		LESS EX	
Top	(F1 (S.W. as	pect) 71		ni	1.
fully	₹F3 (W.N.W.	aspect) 62		52	2
exposed.	(F 5 (E.S.E a	spect) 52		15	5
Sheltered by	(F2 (S.W. as	pect) 11	• • •	5	5
opposite slope.) F 3 (E.S.E. a	spect) 44	• • • •	30) -

In view of the fact that Calluna develops in the main from seedlings which arise a year or more after the fire (cf. p. 135), a certain amount of shelter has already been created by the Ulex when the Calluna first appears. Hence it is not surprising that the latter exhibits a prostrate habit much less commonly, though here again the effect of increased shelter is clearly exhibited (cf. Table VII).

TABLE VII.

Percentages of Completely Prostrate Calluna on Burnt Areas.

LOCALITY.	EXTREME EXPOSURE (TOP OF SLOPE).	LESS EXPOSURE (BASE OF SLOPE).
P1	53	7
F 3	40	39
P 5	26	nil

Prostrate shoots of *U. nanus* were tied up in a vertical position in considerable numbers, and these showed a marked tendency, after some months, to die away at their tips. Several of these exhibited a downward curvature of the tied-up shoot, the tips in these cases remaining healthy. A similar dying back of the tip was also observed in tied-up *Erica cinerea*.

Since Ulex europæus is practically confined to the valleys, where it normally finds sufficient shelter to develop in the usual way, good examples of the prostrate type of this species are almost absent except on the land-slides, where they are in part due to rabbit-trimming (cf. below). There can be no doubt that there is a much greater tendency towards the production of prostrate branches in U. nanus than in U. europæus. Indeed careful investigation has shown that all specimens of the former, even those with a tall upright stem found in the valleys (3, p. 151), possess a creeping branch-system whose remains can be found hidden among the humus at the base of the erect shoot. These plants have then in all cases exhibited initial prostrate growth.

In U. europæus, on the other hand, the tendency is towards the upright habit, and consequently the tall-growing specimens in the valleys do not possess branches prostrate on the ground, but realise the cushion-habit, in the more exposed situations, on branches which have over-topped the surrounding vegetation. Where plants of U. nanus have produced erect shoots, which become exposed, they likewise assume this densely branched character, either forming typical cushions or exhibiting a more or less corymbose arrangement of the upper branches, features which may perhaps correspond to differing conditions of exposure. The cushion-habit of such branches (Pl. I, Phot. 5) is due to the regular dying away of the exposed tips (in *U. europæus* this amounts to $\frac{1}{2}$ - $\frac{3}{4}$ inch in each annual increment) and the resulting stimulation to growth of the axillary buds immediately below. At the same time the spinous branches are shorter and all the parts are smaller (cf. a and b in Pl. I Phot. 7). In nonexposed branches (erect non-exposed type, cf. below) irregular dying back occurs, but the axillary buds sprouting below develop unequally and their average annual rate of growth is much greater; also the main axes of the branches tend to persist and often grow for more than one season. In other words the growth of exposed shoots is almost exclusively sympodial, whereas sheltered specimens are in

¹ It was previously thought that procumbent branches were generally absent in the upright form (cf. 3, p. 152).

part monopodial. Probably correlated with the dense character of the periphery, the interior of these aerial cushions exhibits an early dying away of the lateral appendages, so that only the outer parts appear green.

In marked contrast to the wind-trimmed shoots are such as grow in the shade and shelter afforded by other plants or branches (shade-type, cf. below). The chief features of these are their flexibility and the slender nature of all the appendages. In concluding our consideration of the growth-forms of Ulex attention may be called to the fact that all the different types may occur together on different parts of the same plant, where these are differently circumstanced. We may therefore distinguish the following types:—(1) the prostrate type, rarely observed in U. europæus; (2) the intermediate type, with both prostrate and upright branches (3, p. 152), only observed in U. nanus; (3) the erect non-exposed type; (4) the aerial cushion type; (5) the corymbose type, only observed in U. nanus; (6) the shade-type.

(3) Growth-forms on the Land-slides.

Some of the most striking growth-forms are to be found on the bare areas left by land-slides on the N.W. slopes of valley B (see Fig. 1), but these appear to be due to the combined action of wind and rabbits. Perhaps it may be well to mention at this point that the growth-forms enumerated in the preceding section are due entirely to exposure, the actual dead tips resulting from this influence having been observed in numerous instances; moreover, in the case of the ærial cushions their height above the ground precludes the agency of rabbits. Over most of the area the grasses and sedges alone appear to be attacked by these animals, but near their burrows which are mainly situated in the land-slides nearly all the species present seem to be nibbled. This is apparently not done for the sake of food, since the detached tips are often found scattered around. Although the areas under consideration are situated on the sides of a valley, this runs in the direction of the prevailing winds, and further, owing to the open character of the association. little shelter is afforded, so that wind probably plays a considerable part in the production of the growth-forms now to be discussed.

Ulex europæus, U. nanus, Calluna and Erica cinerea all exhibit cushion or mat-like forms appearing as extreme examples of the type found on burnt areas. It is of interest to note that these cushions of U. nanus have been observed producing numerous

adventitious roots from the branches in contact with the soil. A unique instance of the prostrate type is afforded by the young plants of *Pinus sylvestris* in which the main axis appears to have been bitten off by rabbits, whilst the laterals, probably under the influence of the wind, continue for a time to grow horizontally (Pl. I, Phot. 1). Of the numerous young trees of *P. sylvestris* on the land-slides several show that they possessed the same prostrate habit in young stages, the present main axis being one of the laterals that has assumed a vertical direction.

The effect of nibbling upon the Calluna is very striking, and results in extremely dense branching which, in the case of the more erect specimens, gives the plant the habit of a Japanese dwarf tree (Pl. I, Phot. 2). Where old cushions of Ulex europæus, bitten in this way and simultaneously subjected to considerable exposure, have grown in the upward direction, the cushion-habit is retained throughout, whereby various grotesque forms are assured (Pl. I, Phot. 6).

C .- COLONISATION.

(1) Cryptogamic succession.

Amongst the first new arrivals to appear on a burnt area are These are Cystococcus humicola Næg., forming dark green granules in most of the countless small depressions of the soil, and gelatinous forms (Glæocystis vesiculosa Næg., Trochiscia aspera Hansg. and Dactylococcus infusionum Næg.1) constituting a thin. macroscopically invisible layer over the greater part of the surface. At a very early stage Ascobolus atrofuscus2 is to be found growing over the whole gelatinous layer, its hyphæ ramifying profusely in the latter and especially enveloping groups of the Cystococcus in a dark pseudoparenchymatous investment. These enveloped groups, when viewed with a lens, appear as numerous minute rounded protuberances of an olive-brown colour which, when present in large numbers, give a velvety texture to the surface. The apothecia arise in quantity from the hyphæ generally and do not seem to develop from the threads more intimately associated with the Cystococcus. The same fungus is common on burnt areas of all ages, as well as on parts of the mature heath. Another fungus, rare and local in its distribution, is Humaria melaloma which has only been encountered on one of the burnt areas in the early part of the year.

¹ This is generally regarded as a stage of Scenedesmus obliquus Kuetz.

³ For the identification of these Fungi, the authors are indebted to Mr. J. Ramsbottom, M.A., and for the identification of Mosses to Dr. F. Cavers.

We have noticed that in the first stages the Cystococcus appears as dark green granules in the depressions; on slightly older burnt areas (e.g., F 2, F 3) the dark colour of these granules gives place to a pale yellowish-green, due to the envelopment of such Cystococcusgroups by the colourless hyphæ of an additional fungus, as an incipient stage in lichen-formation. Of the lichens that arise in this way on relatively young burnt areas Cladonia delicata Ehrh. is at first the only one to be found in fruit, but others in the sterile condition are probably associated with it. The small scale-like lobes of their pale green thalli form numerous patches on the soil and these are dominant for some years on the barer parts, until in fact the Phanerogamic vegetation begins to close, when they become subordinated to other forms or completely disappear.

Simultaneously with the gradual development of the Lichen-flora we have an increase in the Glæocystis and its associates over the general surface, these, together with Mesotænium violascens De Bary, forming increasingly conspicuous jelly-like lumps of a dirty green colour which occupy practically the whole surface left bare by other forms.¹ Such lumps are generally visible with a lens about two years after the occurrence of a fire and gradually increase in bulk, so that approximately three years later they are discernible on close observation to the naked eye. Finally, in the tall Calluna the gelatinous forms occur as conspicuous masses from a quarter to half an inch in diameter. It will be realised that, as regards the cryptogamic flora, the association is closed almost from the first.

Apart from the forms already mentioned the only other algae encountered on the burnt surface are *Hormidium flaccidum* A. Br. and *Zygnema (Zygogonium) ericetorum* Hansg., both of which, and particularly the latter, are rare and local in their distribution.²

Some three or four years after a fire Cladonia delicata becomes associated with C. furcata Hoffm., C. Flærkeana Fr. forma trachypoda Myl., C. pyxidata Fr., C. squamosa Hoffm., and rarely C. sylvatica Nyl.; of these five C. furcata seems to be the first to appear. As the phanerogamic vegetation becomes more and more closed, C. sylvatica increases in amount and with it, in these later stages, are found C. pyxidata and C. coccifera Schær. The lichens appear to reach their maximum development, both as regards amount and variety of species, in the phase which we have termed

¹ The absence of diatoms in the algal covering is noteworthy.

² Although examined at different times of the year there appears to be no seasonal difference in the constitution of the algal covering.

"poor Calluna." On certain neighbouring heaths (e.g., at Frensham, 3, p. 155) this condition, with a poor growth of Calluna and an abundant lichen-flora, in which a species of Cladonia (probably C. sylvatica) predominates, appears to be a relatively permanent state. In the tall Calluna on Hindhead C. sylvatica is the only common lichen, apart from a fairly abundant growth of Parmelia physodes Ach. upon the older stems and branches and a small amount of Cladonia pyxidata (cf. 1, p. 68).

Mosses are to be found in the very earliest stages and these include Ceratodon purpureum Brid, which is very abundant, together with small patches of Tortula subulata Hedw. and Funaria hygrometrica Sibth. In slightly later stages these are associated with Campylopus brevipilus B. & S. and Polytrichum piliferum Schreb. The mosses, although locally forming continuous sheets, are not uniformly distributed over burnt areas as is the case with the algae and lichens. About two or three years after a fire Ceratodon tends to disappear, and for a time mosses are quite insignificant as compared with the abundant lichens. It is interesting in this connection to note that Elgee writing of the "fat moors," says that some swiddens have been almost covered with lichens, chiefly of the genus Cladonia (1, p. 45).

In the final stages of the heath however, mosses are abundant; the most conspicuous forms are Hypnum cupressiforme L. var. ericetorum B. & S., Leucobryum glaucum Schimp., and Dicranum scoparium Hedw., the first-named in particular attaining a great development where light penetrates through the Calluna-canopy.

On the land-slides on the south-east slopes of the central ridge, where the soil consists of numerous pieces of broken rock mingled in a sandy matrix, the terrestrial form of Zygnema (Zygogonium) ericetorum Hansg. forms extensive dark purple sheets binding together the surface-layers of the sand, but, possibly owing to the mobile nature of the substratum, it does not as yet appear to have led to any permanent fixation of the surface. There is, however, reason to believe that this alga is of relatively recent occurrence on the land-slides. This form is peculiarly suited to such arid situations, for not only are its cells remarkably thickwalled, but, in conditions of drought, it exhibits various modifications tending to prevent excessive loss of water and at the same time permitting of rapid recovery when wet weather sets in. At one or two points extensive patches of the Z. ericetorum are becoming overgrown by bright green filaments of Hormidium

flaccidum A. Br., which hence plays the role of a secondary coloniser.

The only other cryptogams which play an important part on the land-slides are the lichen Bæomyces rufus DC. and Polytrichum piliferum, whilst the fungus Clavaria argillacea Pers. has a scattered distribution in the autumn. Both the alga Z. ericetorum and the lichen Bæomyces are encountered on burnt areas, but here they are almost confined to the sandy surface exposed by the creation of paths.

Attention may be drawn to the fact that the cryptogamic flora, both in its constitution and in the succession of phases recalls the description given by Græbner in his work on the North German heath (4, p. 82 et seq.). The species involved are in part the same.

As has been pointed out by Warming (7, p. 208), Cladonias are often highly important peat-formers on heaths, and we have noticed that the lichen-flora does not reach any considerable development until four or five years after a fire. Estimations of the humus from burnt areas of various ages show no great difference in the amount during the first years subsequent to burning. It may well be, therefore, that Calluna remains puny, especially upon the slopes, until there is a sufficient accumulation of peat to admit of its vigorous development, and that this peat is largely produced by the abundant Cladonia-flora in later phases. As a matter of fact, measurements indicate that the average rate of growth of the Calluna, where the peat is deep, is more rapid than where the latter is shallow (poor Calluna).

(2) Phanerogamic succession.

Amongst early herbaceous colonisers seedlings of Carex pilulifera are universally frequent, sprouting stools as already stated being relatively rare. Other common colonisers are Polygala vulgaris, Rumex acetosella, Galium saxatile, Potentilla erecta, Epilobium angustifolium and Cuscuta epithymum, those with windborn seeds or fruits naturally appearing first. It is to be noted that Rumex acetosella, which on other heaths is often locally dominant after burning, is here never abundant over extensive areas, whilst Holcus lanatus is almost absent as a coloniser. The only grasses, of which seedlings are found in any quantity, are Aira flexuosa, Festuca ovina, Poa annua and Agrostis vulgaris.

¹ Apart from the hosts already mentioned (3, p. 159) this parasite has been found on Pteris, Aira, Triodia, Molinia, Agrostis, Erica tetralix, Potentilla erecta, Galium saxatile and sprouting Betula.

DISTRIBUTION OF SPECIES ON DIFFERENT PARTS OF THE HEATH.

Species.	cu.	Path.	F1.	F 2.	Punch Bowl. F 3.	F 3. W.N.W	F 3. E.S.E.	F 5.
A.—PHANEROGAMS:— (a) Trees and Shrubs. Betula pubescens Calluna vulgaris Cratægus monogyna Cytisus scoparius Erica cinerea	o d r r	_ _ _ 1	r vr-lc _ r-lc	rc - vc	1c - 1c	r a —		c - vc
,, tetralix Ilex aquifolium Pinus sylvestris Pyrus aria , aucuparia Rhamnus frangula	1 0 f f rr 1	— — — — — — — — — — — — — — — — — — —	r 	lc vr — vr —	r 	1c —		- vr - -
Rubus fruticosus Ulex europæus ,, nanus Vaccinium myrtillus (b) Herbs.	l sd la	f vc c lc	lc vr c	lc c vc lc	c vr r c	vr r vc vr	vc vr	o vc rr
Agrostis vulgaris Aira flexuosa Blechnum spicant Carex pilulifera Cerastium tetrandrum Cuscuta epithymum	r 0 lr f —	f lr r lc	la r f	rr - rr - r	c f lc	1f f 1c 1	- - - - - - - 1	Ic If
Epilobium angustifolium Epilobium montanum Festuca myurus, ovina Galium saxatile	- - -	r f f	vr vr r f r-f	- If Ic	f - -	vr - r r	-	
Hieracium boreale (agg.) Holcus lanatus Hypochœris radicata Luzula campestris Molinia cœrulea	 - - - -	f f r f	vr vr r	vr vr lc	- - - - -	- vr - r	- - - - -	- - - -
Nardus stricta Poa annua Polygala vulgaris Potentilla erecta Pteris aquilina	vr vr vr 1	f r r f la	vr r r	rc r vc	 la	lc lf r r	$ \frac{-}{f} $	- f c
Rumex acetosella Scirpus cæspitosus Senecio sylvaticus , vulgaris Taraxacum officinale Teucrium scorodonia Triodia decumbens	- - - vr	f vr - vr f f	lc vr vr vr	r If 	- - - - - - - -	vr		
Viola riviniana	-	0	rr	-	1 -	1	-	-

Symbols used to denote frequency:—d = dominant; sd = sub-dominant; a = abundant; vc = very common; c = common; b = locally common; f = frequent; rr = rather rare; r = rare; vr = very rare; o = occasional.

TABLE VIII-continued.

Species.	ÇU.	Path.	F 1.	F 2.	Punch Bowl. F 3.	F 3. W.N.W	F 3. E.S.E.	F 5.
B.—Mosses:— Campylopus brevipilus Ceratodon purpureum Dicranum scoparium Funaria hygrometrica Hypnum cupressiforme var. ericetorum Leucobryum glaucum Polytrichum piliferum Tortula subulata			c-r la — If	c-r - - vr vr	f a c o	la lc lc	la o	f -
C.—LICHENS:— Bæomyces rufus Cladonia coccifera ,, delicata ,, Flœrkeana f. trachypoda Cladonia furcata , pyxidata , squamosa , squamosa , sylvatica Parmelia physodes	- r - 1 -? 1c - c c	f .	?		? ? !c ? vr? —	vr - ? f? c? r ?	f? c r ? r —	c c r r
D.—FUNGI:— Ascobolus atrofuscus Clytocybe sp Humaria melaloma Mycena polygramma E.—ALGÆ:—	f -	=	a f f	a f —	?	a 	a 1	vc
Cystococcus humicola Dactylococcus infusionum Glœocystis vesiculosa Hormidium flaccidum Mesotænium violascens Trochiscia aspera Zygnema ericetorum	- c lr c	- - - - - 1c	a vr a — f	vr a 	, ,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,	o a lr rr c	o a ? rr c r	o a ? rc c

In addition to the above, the following species have been found exclusively in the neighbourhood of paths:—Rubus idæus (1), Achillea millefolium (c), Agrostis alba (f), Aira præcox (f), Anemone nemorosa (lc), Anthoxanthum ordoratum (o), Bromus mollis (r), Campanula rotundifolia (f), Carex binervis (c), Centaurea nigra (rr), Cerastium viscosum (r), Chrysanthemum leucanthemum (vr), Cynosurus cristatus (c), Dactylis glomerata (r), Digitalis purpurea (rr), Erigeron canadense (r), Festuca rubra (c), Holcus mollis (o), Juncus effusus (l), Lolium perenne (c), Orchis maculata (vr), Pedicularis sylvatica (vr), Plantago major (vr), P. lanceolata (f), Rumex crispus (vr), R. obtusifolius (vr), Scilla nutans (rr), Solidago virgaurea (f), Spergula arvensis (vr), Stellaria graminea (f), Trifolium pratensis (o), Veronica officinalis (f), Viola tricolor

Of the shrubby members, seedlings are commonly found only in the case of Ulex nanus, Calluna, and Erica cinerea. Large numbers of seedlings of the first-named appear almost immediately after a fire, but the vast majority of these subsequently die. Thus. on F 1 (burnt June, 1913) numerous healthy U. nanus seedlings were found in the April succeeding the fire; two months later (in June) from five to ten per cent. of these were dead, whilst in October the number of dead seedlings was still larger. abundant U. nanus seedlings previously recorded on F 3 (3, pp. 156,157) in January, 1912, were represented by only a few survivals The Erica cinerea and Calluna seedlings which in June, 1914. appear slightly later are very numerous, as shown in Table IX, and a large percentage of these are destined to survive. It is to be noted that the burnt stools of these two forms rarely rejuvenate (p. 119), and therefore their presence in the mature heath depends largely on the survival of seedlings. Moreover, since the U. nanus mostly rejuvenates, it not only obtains a start over the laterappearing Bricas and Callunas, but the shoots, growing as they do, from an already established root-system, will at first develop much more vigorously than the seedlings of the other two genera.

TABLE IX.

NUMBER OF SEEDLINGS PER TWENTY-FIVE SQUARE FEET OF BURNT AREA (APRIL, 1914).

Locality.	Ulex nanus.			Calluna.	Erica cinerea.		Vaccinium.		
F 2		430		574	•••	19,068	•••	6	
F 3		87	•••	4,641	•••	11,513	•••	-	

Seedlings of Erica tetralix are rarely found on newly burnt areas except where these adjoin the damper depressions in which this species occurs in some quantity. Vaccinum seedlings are also sparse (see Table IX), possibly in part owing to the paucity of the peat, in part to the fruits being largely dispersed by birds which do not settle frequently on the burnt areas.

The extent to which seeds of the typical heath representatives, already present in the peat, play a part in colonisation is uncertain (cf. 5, p. 179), but it may be mentioned that such seeds do occur, though only those of Erica cinerea have been found in any quantity. It is quite probable that the hard caked crust, formed by the charred peat, may retard colonisation by seeds falling on the surface. An experiment with cress seeds showed that these germinate quite readily on the broken charred surface, but of an equal number sown

where the crust was left intact, the radicles of the majority failed to penetrate; moreover, it was noticed that the few successful ones were those which had lodged in small crevices. We may add that the radicles of many of the unsuccessful seedlings exhibited an upward curvature, away from the burnt crust. Possibly the earlier appearance of *U. nanus* seedlings, as compared with those of the other heath representatives, is due to a greater toleration of the inhospitable surface. It is probable that the gradual increase in the coating of gelatinous algæ may after some time facilitate the penetration of the radicles of germinating seedlings.

The rate of growth of the shrubby members depends largely upon conditions of shelter, and consequently corresponds more or less to the phase of development of the heath. Thus, as already mentioned, the upright shoots of *U. nanus* often exhibit dying back on burnt areas, whilst the prostrate shoots grow at an average rate of slightly over two inches per annum. Later, when more shelter has been established (CUE phase), the average rate of growth of the upright shoots (based on a large number of specimens) is 2.5 in.; in the final (CU) phase, the growth of such shoots amounts on an average to 1.5 in. The Callunas and Bricas develop later than the Ulex nanus on the burnt areas, and related to the shelter already established, their growth is at first very rapid. In the CUE phase the average rate of growth for Calluna is 1.235 in., and in the CU phase 1.154 in. It will be seen that the falling off in the rate of growth of older specimens of Calluna is much less marked than in Ulex nanus which is probably correlated with the fact that tall specimens of the latter develop as isolated plants in the CU, whereas the tall Calluna grows en masse.

As the shrubby members become established, most of the herbaceous forms are ousted, Aira flexuosa, Molinia cærulea and Carex pilulifera being almost the only ones that remain in any quantity; Polygala vulgaris and Potentilla erecta are occasionally present, whilst Blechnum spicant is a rare form occupying the damper hollows. The ultimate phase with dominant Calluna and Ulex nanus often includes drawn-up Erica cinerea and E. tetralix, with etiolated specimens of Pteris and Vaccinium (cf. 5, p. 178). In the wetter parts with abundant peat, where the Vaccinium grows as rapidly as the Calluna, the former becomes a co-dominant and exhibits no etiolation. Actinometric data show that the light-intensity at the soil-level in the tall Calluna-zone is only about one-fifth of that outside.

Spontaneous colonisation, mainly by Pinus and Betula, is a prominent feature, but owing to the felling of these over the greater part of the heath, on reaching a certain size, they fail to lead to a further phase. At the south end of the common however, such colonisation has not been interfered with, so that a definite woodland (in which Pinus sylvestris predominates) has been established; reference to the survey-map of 1895 shows no indication of woodland here at that time. That the Hindhead Common may formerly have been occupied by woodland is suggested by the abundance of woodland plants (Anemone nemorosa, Viola riviniana, Orchis maculata, etc.) in the valleys.

In conclusion we may call attention to the close resemblance, both as to the successive phases and final condition, which the flora of this southern heath bears to the "thin moors" of North-East Yorkshire, as described by Elgee (1, pp. 65-76).

D.—SUMMARY OF SUCCESSION-PHASES.

- Phase 1. Characterised by the presence of algæ (Cystococcus, Glæocystis, Trochiscia), Ascobolus atrofuscus, seedlings and sprouting stools of Ulex nanus.
- Phase 2. Algæ and soredial groups; mosses (Ceratodon, Funaria); sprouting stools of U. nanus, etc.; seedlings of shrubby members; also a number of herbaceous plants, especially Aira, Carex pilulifera, Polygala, Galium, Rumex acetosella and Cuscuta; many of the U. nanus seedlings dying away.
- Phase 3. Lichen-phase with thalli of Cladonia spp.; algæ as in Phase 1, together with Mesotænium; increased phanerogamic vegetation.
- Phase 4. (a) Vigorous Calluna, Ulex nanus, Erica, with numerous lichens; algæ as in Phase 3; disappearance of most of the herbaceous species (CUE phase). (b) (Poor Calluna) Similar to a, but with poorly developed shrubs and still more numerous lichens—this type is more particularly associated with the steeper slopes.
- Phase 5. (a) Considerable development of peat, Calluna dominant and Ulex nanus sub-dominant; frequent Hypnum and Leucobryum, Cladonia sylvatica, Parmelia physodes, Mesotænium and Glæocystis. (b) Similar to a, but with co-dominant Vaccinium and with less pronounced Ulex nanus; very considerable accumulation of peat.

Phase 6. Colonisation by Pinus, Betula, Pyrus, etc.

East London College, December 18th, 1914.

DESCRIPTION OF PLATE I.

- PHOT. 1. Seedling of *Pinus sylvestris* in exposed situation. The main axis has been bitten off by rabbits, whilst the laterals have developed horizontally.
- PHOT. 2. Plant of Calluna showing combined effect of nibbling and exposure.
- PHOT. 3. Two plants of Calluna killed by a fire, showing the superficial position of the crowns. The ground-level is indicated by a black line.
- PHOT. 4. A plant of Calluna which has sprouted after burning, showing the buried crown.
 - PHOT. 5. An aerial cushion of Ulex nanus.
- Phot. 6. Cushion of U. suropæus showing combined effect of nibbling and wind-trimming.
- Phot. 7. Two shoots of U. europæus, (A) from a sheltered and (B) from an exposed situation.

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THE AUSTRALIAN MEETING OF THE BRITISH ASSOCIATION.

II. BOTANICAL PAPERS.

By E. N. Thomas.

THE meeting of the British Association in 1914 will be doubly memorable in that it was held at the Antipodes and at the outbreak of the Great War. The main business of the meeting was sharply divided between Melbourne and Sydney, but special lectures were also given at other big centres such as Adelaide, Brisbane, etc.

The botanical papers included many of special local interest such as those given at Melbourne on the Flora and Ecology of the Environs, and even including one on the romantic "Never-never Land" of the North-West Territory. At Sydney a group of papers was presented dealing with many aspects of the all prevailing gumtree, the genus *Eucalyptus*, which Mr. Maiden has made so peculiarly his own.

PRESIDENTIAL ADDRESS.

The President began his address with a brief survey of the growth of Australian Botany from the foundations laid by Banks on Captain Cook's expedition in 1770 to the establishment of the latest Chair of Botany at Sydney. Curiously enough Banks' invaluable Journal did not see the light for 125 years after it was written, although of course, his collections of some 1,000 species had long been lodged at the British Museum. In 1810 appeared Robert Brown's "Prodromus Floræ Novæ Hollandiæ," which incorporated his own and Banks' plants, and in 1859 was published the "Antarctic Flora," the result of Sir Joseph Hooker's travels. This included not only the description of some 3,000 species but a masterly discussion of the problems of distribution and descent.

The current systematic work is the "Flora Australiensis" of Bentham and Muller, completed in 1878. This recognises two main strains, the one a specialised indigenous flora, the other an Indo-Australian flora best seen in Queensland and the North, and indicative of ancient land connections between Australia and adjacent islands. The mountain flora common to Australia and New Zealand and other southern extra-tropical mountains as also certain American and Mediterranean plants are less easily accounted for. Professor Bower pointed out that the real work of botanists in

the country had hardly begun and that care must be taken to secure its adequate prosecution.

The President then proceeded to consider certain of the Australian plants from the phylogenetic aspect, in particular the Pteridophytes, and finished with a very illuminating presentment of the difficulties of evolutionary investigations.

The peculiar Australasian genus *Phylloglossum* loses much of its phylogenetic interest as an archaic type, if we subscribe to the view which sees in the "protocorm" a biological adaptation to annual growth. Professor Bower shows, however, that we can hardly avoid this conclusion if we compare *Phylloglossum* closely in its habit and mode of growth with what is now known concerning the various species of Lycopodium in particular with *L. inundatum* and the Australian species *L. laterale*, the former of which produces small protocorms each year, while the latter has an embryonic tuber of exceptional size. *Phylloglossum* would seem, therefore, to have carried this tuberous habit to its fullest development and both starts and continues life on geophilous lines.

Professor Bower dwelt at some length on the peculiarities of the Australian members of the ancient type of Ferns so well represented in the Australian flora, and showed that the most perfect demonstration of their archaic character had been built up on a New Zealand fossil Osmundites which furnished the first member of the brilliant series of papers on Fossil Osmundaceæ. The monotypic New Zealand Fern Loxsoma shows characters shared by the isolated Juan Fernandez form Thyrsopteris and by the recently discovered Jurassic fossil Stachypteris Halli. This curious distribution of characters would seem to indicate that they represent relics of a once widespread Filicinean condition. Professor Bower then drew attention to the fact that the isolation of the Hydropterid condition bids fair to be bridged by Professor Lignier's discovery of the heterosporous form Mittagia.

The difficulties of phyletic interpretation which present themselves even among Ferns—in many ways one of the eaziest groups was shown to be largely due to the prevalence of parallel development in phyla of distinct origin. This difficulty is very acute among the Angiosperms, in which no fossil appeal is as yet possible, and in which the "irritating sameness" of their essential features on the one hand and the great adaptability of the multitude of forms on the other, render phylogenetic unravelling almost impossible. The great need here is for a widening of the criteria of comparison which can only be furnished by laborious investigation along new and old lines.

The phenomena of convergence or parallel development force us to consider the working of heredity which makes this possible. It may be well to entertain as a working hypothesis the possibility of the determination or, at any rate, the promotion of heritable mutations by external conditions, which is of course the old heresy of inheritance of acquired characters. We are, perhaps, too prone to force the analogy between plants and animals, and in plants, at any rate, the possibilities of environmental influence on evolutionary development cannot be excluded from consideration.

The President concluded by emphasising the extreme importance of the direct historical evidence of Palæophytology—"the most positive line that we possess in the broad avenue of botanical Phylesis"—which may even enable us to forecast future possibilities with a measure of success.

Morphology and Anatomy.

For Sydney was reserved the honour of the Presidential Address, but the jealously guarded prestige of Melbourne was upheld by the presentment at its meeting of an important paper by Professor Bower dealing with the Matonioid Perns. The author has examined in detail Cheiropleuria bicuspis, a Malayan Fern figured by Sir W. Hooker, and now shown to possess features connecting with Matonia, Dipteris and Platycerium. In the light of Professor Bower's extensive knowledge of the comparative morphology of Ferns, he is able to pronounce on Cheiropleuria as a synthetic type showing perhaps closest relationship to Platycerium but serving to link up these forms in such a way as to suggest their common origin from a Gleichenioid source with Matonia as in most respects the most primitive genus.

A paper on the Morphology and Anatomy of certain pseudo-Monocotyledons by Dr. E. N. Thomas and Miss A. J. Davey, gave a preliminary account of certain pseudo-Monocotyledonous forms. These are characterised by a much elongated "petiolar" region to the cotyledon which is very marked in Conopodium denudatum, etc., and by the early appearance (in Cyclamen persicum before the cotyledon emerges from the seed) of a tuberous swelling which is variously related to the "collet" and which therefore seems to arise in very different morphological regions. Older seedlings, however, prove that the tuber is always formed below the

cotyledonary node, the extraordinary development of the "collet" in the cotyledon being accountable for the apparent variability in the position of the tuber.

The anatomy of these forms is very interesting and Conopodium denudatum and Anemone apennina are remarkable on account of the presence of complete root structure in the lower part of the petiole of the cotyledonary member.

GENETICS.

The meetings of Section K were opened in Melbourne with an address by Miss E. R. Saunders, entitled "The Double Stock: its history and behaviour." There is no record of the double form until the middle of the 16th Century, and we are probably justified in supposing that it did not exist long before that date, although the Single Stock dates back to Greek and Roman times.

The possibility of obtaining doubles from the seed of singles—the doubles themselves being sterile—was not realized for more than a century after their cultivation, and the usual mode of propagation was by slips or cuttings. Suggestions for increasing the number of doubles have always failed under experiment, and the reasons are obvious now that we know their Mendelian relationship. Nevertheless, it is possible by appropriate selection of seed or plants to obtain an increased number of doubles in the bed as a whole.

This was followed by a paper by Dr. Bond, on Sex Dimorphism and Secondary Sex Characters in some Abnormal Begonia Flowers, and on the Evolution of the Monœcious condition in Plants. The author apparently assumes the diœcious condition to be the most ancient, and regards the hermaphrodite as produced in response to insect fertilization with the monœcious as an unstable intermediate condition. Sex differentiation usually occurs in such a way as to give central terminal femaleness and peripheral lateral maleness as in the normal hermaphrodite flowers, and in many inflorescences, and even in abnormal flowers such as those of the Begonia, particularly studied by Dr. Bond. These show associated secondary sex characters such as abnormal floral bracts, etc. The author contrasts the comparative inconstancy of secondary sex characters among plants with the much greater interdependence of these with the primary secondary sex characters among animals. and suggests that this may be due to the much more restricted action of sex hormones among plants.

Mr. R. P. Gregory gave an account of the extraordinarily interesting phenomena associated with Inheritance in certain Giant Races of *Primula*. These giant forms possess twice the normal number of chromosomes both in gametophytic and sporophytic generations, and inasmuch as they prove to possess also a duplication of inheritance factors, hope is entertained that they may help to elucidate the possible relationships between factors and chromosomes.

If we suppose that in the pure-bred diploid race each factor is represented twice, AA, then in the tetraploid race—arising in one case in the F₂ of a diploid cross—each factor is represented four times, AAAA, and there are three distinct hybrid types, namely: AAAa, AAaa and Aaaa, similar or dissimilar in appearance according as a single "dose" is sufficient or insufficient for the development of the character. In any case they are recognised subsequently by their progeny resulting from self-fertilization and giving respectively no pure recessives, one in sixteen recessives and one in four recessives. The ratio 15 dominant to 1 recessive, recall those obtained by Nilsson Ehle in Oats and Wheat, and by East in Maize, but the case of the Primulas differ in that the duplication affects all the characters studied, not merely the factors for isolated characters.

It would be unsafe to conclude that the relationship between factors and chromosomes is thus shown to be a close one, for various reasons, but nevertheless it is probable that further study of these forms will establish a connection.

Systematic Botany and Ecology.

Professor A. J. Ewart and Miss Olive B. Davies gave an Account of the Flora of the North West Territory. This forms one of the contributions resulting from the Barclay Expedition. It considers the Leguminous plants so obtained from the point of view of their economic value, especially their poisonous qualities. Thus Bauhinia has three poisonous species, Crotalaria five—only one of which fortunately is found in this area. It seems probable that Gastrolobium grandiflorum falls under this ban, as also Tephrosia purpurea, but much remains to be done before anything like a complete list can be published.

In an account of the Flora of the Environs of Melbourne, Mr. Sutton showed that there is a very distinct correlation between the geological area and the associated flora, leading to the conclusion that the soil conditions present the dominating factors. Thus the basaltic plain running N.W. and S.W. is characterised by grass steppe with the minimum of trees, while the Silurian area bears a Eucalypt forest formation filled in with scrub. The Tertiary sands are covered with a maquis of Epacrids, Orchids and Myrtaceous plants, while the strand bears the usual halophytic flora.

In a paper on the Australian Ebenaceæ, Mr. Hiern recorded his investigations into the taxonomic value of histological characters within this order, which has long been associated with his name.

Dr. E. M. Berridge discussed the Systematic Position of Casuarina and its Allies, and showed that its once isolated and supposed primitive position has been undermined by the increase of knowledge concerning chalazogamy on the one hand, and concerning the inflorescence, flower and cupule of Fagaceæ on the other. She supports Hallier's original view that the ancestors of the Cupuliferæ were allied to the Rosaceæ.

The series of Eucalyptus papers mentioned above included:—

- 1. "The Species Concept with special reference to Eucalypts," by J. N. Maiden. The author emphasised, with reference to his own detailed work on *Encalyptus*, the importance of obtaining a wide and comprehensive knowledge of a species, which must be treated as a whole if it is to yield satisfactory conclusions. Species correspond to the evidence of our senses, and as such will never be abandoned, although it is obvious that attempts to define our conceptions of species lead to illogical and often ridiculous positions.
- 2. "The Correlation between the Specific Characters of the Tasmanian and Australian Eucalypts," by Mr. R. T. Baker and Mr. H. S. Smith. The authors review their work on Tasmanian Eucalypts in the light of twenty-five years' experience of the genus on the mainland. They see reason to believe that the Tasmanian species are the more recent. Notwithstanding the variety of soils, climates, altitudes, etc., from which the genus has been examined, the authors find that certain very constant botanical and chemical features charcterise the whole genus.
- 3. "Notes on the Evolution of the Genus Eucalyptus," by Mr. N. H. Cambage. In this paper the changing characters of the genus were reviewed from Eocene times up to the present day. They show that the opposite sessile broad-leaved form with transverse venation was the earliest, and that the spread into colder regions was associated with the development of long narrow leaves with parallel venation. This change was accompanied by

changes in shape and dehiscence of anthers and reduction in size of fruit and flower. An interesting metabolic series is also found from pinene as chief constituent of the essential oil of the more ancient forms to the phellandrine of the more modern.

4. "Variation and Adaptation in the Eucalypts," by Dr. Cuthbert Hall. The author describes certain variations and adaptations in the cotyledons of Eucalypts, and while subscribing to the general view that variations and adaptations are very active in the genus, considers that certain of them are more accurately to be described as deviations or fluctuation variations in the sense of de Vries.

Two papers of special local interest were, one by Mr. Fred. Turner on a Botanical Survey of North-East New South Wales, and the other on Types of Vegetation on the Coast in the Neighbourhood of Adelaide, by Professor T. G. B. Osborn.

The north-eastern portion of New South Wales is of especial interest in that it shows a dense luxuriant semi-tropical vegetation composed of Tree Ferns, Palms, giant Sterculias and figs, covered with epiphytic orchids and ferns and laced together with brilliant-flowered climbers. Many of the trees furnish useful economic products such as strychnine, brucine and strychnicene of the remarkable Strychnos psilosperma and the medicinal products of Duboisia myoporoides. The survey has added 69 new species and 12 new genera to the flora of New South Wales.

Professor Osborn's area includes dunes of various degrees of stability as well as salt swamps and marshes, with mangroves along the tidal estuaries. The latter consist entirely of the Leguminous Avicennia officinalis, mixed with Suæda maritima on the shore ward margin. The periodically inundated areas are covered with Salicornia australis and Salicornia arbuscula, while above the tide limit appear also Melaleuca pustulata, Frankenia lævis, and Mesembryanthemum australe.

The characteristic binding plant of the sand dunes is Spinifex hirsutus, while the first colonisers are probably Salsola Kali, Cakile maritima, etc. Associated with Spinifex are Olearia axillaris, Scævola crassifolia, etc., while on the more fixed dunes occur Mesembryanthemum aquilaterale, Leucopogon Richei, Acacia salicina, Muehlenbeckia adpressa and Clematis microphylla. There is distinct evidence of former more abundant woodland on the dunes more remote from the sea where Callitris propinqua, Eucalyptus odorata and Casuarina quadurivalvis still appear.

The shore itself is strewn with the wrack of *Posidonia*, *Pectinella*, *Zostera*, etc., which may form vast accumulations.

An account was given by Mr. Hutchins of Extra-Tropical Forestry in Portugal from the point of view of the future of Australian forestry. The author lays stress on the value of *Pinus Pinaster* as the most free growing tree in Portugal and South Africa, countries comparable to Australia in climate, and points out that the wood of well-grown trees is suitable for every purpose of furniture and house-building, not merely (as generally supposed) for pit props sleepers, etc.

Various other timber trees, such as cork oak, stone pine, Busaco cedar, English oaks, are considered from the point of view of value and growth conditions.

Among the ecological papers should also be mentioned an account given by A. E. Hamilton on the Xerophytic Characters of Bossiæa slopendria, the mature form of which is leafless but seedlings show small vertically set leaves which, however, retain their dorsiventral characteristics while showing stomata on both sides. The winged branches have sunken stomata, and underneath these palisade parenchyma is massed.

A paper on the Climate in Northern Temperate and Arctic Zones during the Latest Pleistocene Age was presented by Professor Gunnar Andersson, and one on the Geographical Distribution of the Sea-grasses, by Dr. Ostenfeld.

THALLOPHYTES.

In a paper entitled "Relationships of Fungus and Alga in the Lichen-thallus," Miss A. Lorrain Smith gave an historical account of the vicissitudes of lichen theories and lichen cultures. She traced the various steps in the experimental proof of Schwendener's theory of its composite nature and showed that the only question at the present day was as to the exact nutritional relation of the two symbionts. The advantage to the fungus is sufficiently obvious but the advantage to the alga is none the less certain, in that it undoubtedly obtains nitrogen and to some extent carbohydrate from the former.

Professor T. Johnson, in a paper on the Contamination of Drinking Water by an Alga and its Removal, claimed that 1-10 lbs. copper sulphate per million gallons of water successfully freed resevoirs of Oscillaria without any injury to man or fish.

He also read a paper on "Potato Scab and its Causes," distinguishing between "powdery scab" due to Spongospora

subterranea and "black scab" due to Chrysophlyctis (Synchytrium endobiotica,

A consideration of the Spores of Basidiomycetes was presented by Dr. Burton Cleland. The author has made a close comparison of the spore characters of the Australian Basidiomycetes. He finds that the arbitrary classification on spore colour in the mass, while convenient for purposes of identification has no systematic value and tends to dissociate closely allied forms. On the other hand the size of the spores seems to be specific within varying limits.

Professor T. G. B. Osborn presented a paper entitled "Some Observations on the Life History of Ophiobolus graminis."

FOSSIL BOTANY.

In an account of the "Vegetation of Gondwana Land," Professor A. C. Seward considered the characteristics and distribution of the Permo-Carboniferous floras of the Northern and of the Southern Hemispheres. They were compared from the point of view of determining the relation of that of the Southern Hemisphere to the older floras of the world, and in connection with the bearing of the facts on questions of climate, etc. Professor Seward also gave an account of the Possil plants discovered by Captain Scott's last expedition in the Antarctic Regions.

Professor Margaret Benson, considered the Recent Advance in our Knowledge of Sigillaria at some length. The most important advance is, of course, the description of structural cone material by the author herself, who has given to it the provisional name of Mazocarpon. The petrified material is allocated to Sigillaria on the grounds of (1) resemblance to Dr. Kidston's Sigillariostrobus ciliatus; (2) association with Sigillaria leaves and bark; (3) resemblance of cone axis and branches to both Zeiller's and Kidston's Specimens.

Miss Bertha Rees briefly described some fossil fruits of small size obtained from the Larigi Logan South Gold Mine at Ararat.

Physiology.

The only strictly physiological paper was that given by Professor Ewart on Oxidase Enzymes.

Professor Ewart takes exception to the use of such terms as "peroxidase," "katalase," "tyrosinase," inasmuch as these names indicate only one of their many reactions. There is also no justification for the distinction usually drawn between the oxidase and peroxidase classes of ferments, and their supposed fractional

precipitation with alcohol may be merely the result of attenuation. The oxidases of the beet and potato appear to be related to one another and to be among the strongest plant oxidases; carrot and parsnip oxidases are much weaker; malt diastase and papain still more so, and pepsin has no oxidase reaction other than a weak peroxidase reaction with guiacum. Strong metallic poisons will arrest the action of organic oxidases or destroy them (apple, potato carrot, parsnip) if rapid penetration is assured. Hence the organic oxidases are possibly proteids, with or without metals in basic or acid combination. In general, oxidases, whether organic or inorganic, may vary from strong to weak. The strong will cause direct oxidation from the oxygen dissolved in a watery solution, the weak will transfer oxygen from labile oxygen compounds such as hydrogen peroxide, or will use dissolved oxygen in the presence of sensitisers such as sodium chloride. It is possible therefore that the sodium chloride always present in the ash of plants may not be an entirely useless constituent, but may exert a stimulatory or controlling action on plant metabolism in connection with special oxidation or in respiration in general.

Joint Discussions.

The section also met for joint discussions on two occasions. In Melbourne, in conjunction with Section D, a discussion was held on the Nature and Origin of Species. It was opened by Dr. Rendle, who maintained that not sufficient evidence could be produced of the existence of the hybrid forms suggested by Lotsy to be the source of new species by subsequent segregation. Further, Dr. Rendle tests all theories of origin of species by the suitability of the new form to its environment, and therefore he is unable to support Lotsy's view, in that there is no suggestion that such new forms are more suited to the environment and therefore even if produced they are not likely to persist. A similar criticism applies to sports, as it is held that marked changes would be detrimental and therefore exterminated in nature.

The mutations of de Vries do not appear to differ in kind but only in degree from the individual fluctuations which are usually non-heritable. It is believed that each species represents the resultant of a number of slight individual variations rather than of a sudden mutation.

In Sydney, Sections K, C, D and B held a joint discussion on Past and Present Relations of Antarctica in their Geological, Biological and Geographical Aspects, in which Professor Seward took part. I cannot close this brief account of the meetings of Section K, without reference to the very interesting visit that some members were able to make to the Government Experimental Station at Dulacca, where Dr. Jean White and her staff are endeavouring to cope with one of the most difficult practical problems of Australia. One-fifth of Queensland is said to be under the dominance of the terrible pest, Prickly Pear, and its inroads continue at an alarming rate.

Dr. White's long lines of experimental plots for testing the efficacy of different poisons were the admiration of all who saw them, and the laboratory attached now makes possible, investigations into the physiological aspects of their application, so that there is every hope that results of considerable economic importance may accrue.

FOREIGN POLLEN IN THE OVULES OF GINKGO AND OF FOSSIL PLANTS.

By BIRBAL SAHNI,

Emmanuel College, Cambridge.

[WITH PLATE II].

HILE examining some material of young Ginkgo ovules from Montpellier, I was struck by the very frequent presence, in the pollen-chamber, of large pollen-grains with two wings, very different from the normal unwinged grains of Ginkgo. Of he ovules investigated, about a dozen in all, no less than eight contained these foreign pollen-grains, which are characterised by prominent "wings" with reticulate markings like those on the bladders of pine pollen; in both microspores and tubes starch-grains are abundant (Plate II, Figs. 1 in one case two evanescent prothallial cells were seen to features clearly indicate the Abietineous nature of the po

One of the grains has actually put ouft-hand on wice as long as its own diameter, and, what is more striking Female protecting. 2 as if part of the tube had just penetrated grain with its tube penetrated attemptions on the wings.

Recently Professor Jeffrey (Bot. Gaz the series. Pollen-tube w. t. A has called attention to what he describes denclosed in the grain. Tr. The I am, however, unable to confirm this observations, and the series of the series of the series. Pollen-tube w. t. A has called attention to what he describes denclosed in the grain. Tr. The I am, however, unable to confirm this observations of the series.

of the same tube, however, seen in the next section of the series (Fig. 3), is bent sharply away from the nucellus, as if it had met an obstacle. This makes the penetration doubtful. The growth of the tube is away from the floor of the pollen-chamber.

The pollen-chamber of one of the ovules, in addition to a couple of winged grains, also contains two smaller, wingless, round ones (Fig. 4); a third type of pollen, apparently belonging to a third species, and differing from these in its oval shape and smaller size, was seen in different ovules (not photographed). Neither of the two latter kinds of pollen shows any sign of germination; each contains either one or two nuclei and none of them appear to belong properly to Ginkgo. It has not been possible to ascertain whether there were any fertile male Ginkgo trees in the neighbourhood of the tree from which the ovules were collected.

We have here an interesting case of ovules containing foreign pollen from as many as three distinct species, one of the grains being in an advanced stage of germination. Among living plants such an occurrence has not, so far as I am aware, been hitherto recorded. Of course, the chance of foreign pollen effecting an entrance into the pollen-chamber of Ginkgo is not so remote as may at first appear. As in many Conifers, so also in Ginkgo, the pollen-collecting mechanism is a drop of liquid, exuded from the micropyle and subsequently sucked in again. In these circumstances any pollen-grains or other foreign bodies which are arrested by the "stigmatic drop" and are not of too great a size may find their way into the pollen-chamber. Especially in the case of a dicecious tree like Ginkgo, away from its home, and in the usual conditions in which it is grown in the West, perhaps there would be even more chance of foreign than of normal pollen reaching the ovules. In fact, one may well be surprised that medicate ces this kind have not been observed, for xanipie, in the several genera of Conifers (Taxus, Cephalotaus, Juniperus, Cupressus, Sequoia, etc.) possessing minated jollen mechanism.

As Profess of de Vd remarked—and herein lies the chief interest of them the in a similar example were found in a fossil state, it would is belirobability lead to a reference of the pollengrains are number of the same species. The only record of plants known to me is that by Professor In Sydney, Sections K, bermum akenioides figures three foreign Past and Present Relation or les gouttelettes collectrices des ovules des

Biological and Geographical Armandie, t. 24, 1911, p. 51. took part. Soc. Bot. II, 6, 1904, p. 376 and Pl. 42, pollen-grains—found by him "in but a solitary instance"—in addition to a large multicellular grain which was probably the true pollen of Stephanospermum. A comparison of our Figs. 3 and 4 with Professor Oliver's Fig. 15 is interesting. In both cases the pollen-chamber contains foreign as well as normal grains, but while in the former the germinating pollen is known to be foreign, in Stephanospermum the fact that the large grain had germinated went in support of the assumption that it belonged properly to that plant. Had the sections reproduced in Figs. 3 and 4 been from a fossil seed, in the absence of data pointing to the contrary the temptation to assign the germinating grain to the plant in whose ovule it was contained would have been almost irresistible. There is, however, no reason for throwing any doubt upon the diagnosis of the pollen in the fossil seed described by Professor Oliver.

Nevertheless, the present note will serve at least to demonstrate that the mere fact of germination cannot be used in support of conclusions regarding the identity of fossil pollen-grains found enclosed in ovules.

Although perhaps it is not surprising that a pollen-grain should be able to germinate in a foreign ovule, it may be of interest to know at what stage of its growth the (presumably) chemical influences of the ovule arrest the further success of the stranger. Is the ultimate failure occasioned by an active repulsion exercised by the ovule, or is it due simply to a passive inhospitality? Artificial pollination experiments, on a convenient plant like Taxus, might be of some use.

I wish to express my thanks to Professor Seward, at whose suggestion this note was written.

THE BOTANY SCHOOL.

CAMBRIDGE.

May, 1915.

EXPLANATION OF PHOTOGRAPHS ON PLATE II,

ILLUSTRATING MR. SAHNI'S PAPER ON FOREIGN POLLEN IN THE OVULES OF GINKGO.

Fig. 1. Ginkgo. Median longitudinal section of young ovule. Two foreign pollen-grains in pollen-chamber, the left-hand one showing the two large wings, the other lying in a different plane. Female prothallus in early free nuclear stage.

Fig. 2. Same ovule as above, the right-hand grain with its tube penetroof ing (?) the nucellus. Starch grains. Reticulate markings on the wings.

Fig. 3. Same ovule, next section of the series. Pollen-tube wat. A nuclei; a third nucleus is seen in Fig. 1, still enclosed in the grain. Tr. The reflexed.

Fig. 4. Another ovule. Four pollen-grains—two wings alating land in

A DISEASE OF PLANTATION RUBBER CAUSED BY USTULINA ZONATA.

By F. T. BROOKS, M.A.,

Senior Demonstrator of Botany, Cambridge University; formerly Government Mycologist, Federated Malay States.

[WITH SIX FIGURES IN THE TEXT].

Introduction.

COON after arriving in the Federated Malay States at the beginning of 1914 the writer frequently saw a disease of rubber trees which had not hitherto been recorded in Malaya, the disease affecting primarily the collar and root system of the trees. Preliminary investigation shewed that the trouble was probably caused by a fungus, as hyphæ were abundant along the junction of diseased and healthy tissues. The characters of this disease were different from those of the root diseases caused by Fomes semitostus (now more correctly named Fomes lignosus), Sphærostilbe repens and Hymenochæte noxia, but it was not until towards the end of the year that I found the fructifications of the causative fungus, which proved to be Ustulina zonata (Lev.) Sacc. This fungus is the cause of a common root disease of tea in Ceylon (4), and although Petch (5) wrote in 1911 that "it is not yet certain that Ustulina causes root disease in Hevea," he pointed out in 1914 (6) that several cases of Ustulina on rubber had been reported in Ceylon in fields where Hevea had been planted among tea which had subsequently been allowed to die out. This is the only reference to the occurrence of Ustulina zonata on rubber I have been able to find in published accounts of the diseases of Hevea brasiliensis, and no general account of the manner in which it attacks this host has hitherto appeared. The disease has not yet been recorded on Hevea in Java, Sumatra, or Borneo.

FIELD OBSERVATIONS.

The part of the rubber tree chiefly affected by this disease is the collar, which is usually attacked first on one side only. In this region the bark dies and the wood below becomes brown. As the dead tissues break away a shallow depression is often formed on one side of the trunk at soil level. Neighbouring lateral roots and portion of the tap root immediately below the collar are often Past and in the same manner, and in advanced cases the disease Biological at the trunk to the height of two or three feet. If the took part.

diseased tissues are exposed, conspicuous black lines (cf. Fig. 1) about $\frac{1}{32}$ inch in diameter are often seen near the limits of the affected parts, though these lines are not invariably present. These narrow black zones occur more frequently in the wood than in the bark and their course is rather irregular. No external mycelium has been found associated with roots suffering from this disease, hence it is readily distinguished from the root troubles caused by

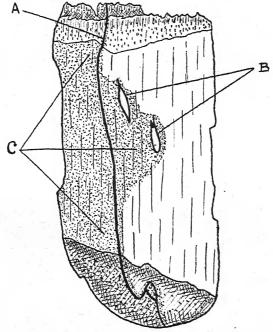


Fig. 1. Ustulina zonata. Piece of rubber wood taken from the collar of an affected tree shewing black zones (natural size). A, long black zone near limit of diseased wood. B, small black zones forming islands some distance from the chief black line. C, diseased wood with brownish discolouration.

Fomes semitostus (Fomes lignosus) and by Hymenochæte noxia. The absence of rhizomorphic strands between the bark and the wood distinguishes the affection from that caused by Sphærostilbe repens, the black lines in the tissues often associated with Ustulina zonata being chiefly found in the wood and differing in nature from rhizomorphic strands, as will be shewn below.

This disease, which is by no means uncommon in Malaya, principally affects old trees, and some of the finest specimens of plantation rubber 14 to 16 years of age have succumbed to it. A few trees 5 to 6 years old have also been attacked by it. The disease has been found both on flat and on undulating land in

several parts of the country. It is, however, only in the few estates where groups of trees have been killed by it that serious damage has yet been done by this fungus.

As the fungus progresses in the collar and root system of the tree, the foliage becomes thin and the branches commence to die back; the tree gradually dies unless successfully treated in an early stage of attack.

Fructifications of the fungus appear on dead tissues of the collar and exposed roots of affected trees to which they are usually closely adpressed. The fruit-bodies, which were found on several occasions on diseased rubber trees in various parts of the country towards the end of 1914, are plate-like in form and grey brown to blackish in colour. The fructifications are easily overlooked, especially in the earlier stages of development, for the colour is not unlike that of the soil on many estates. The difficulty of distinguishing the fungus is further increased in wet weather because the fructifications developing near the ground become splashed with mud. Fig. 2 shews a fruit-body which was taken from a diseased

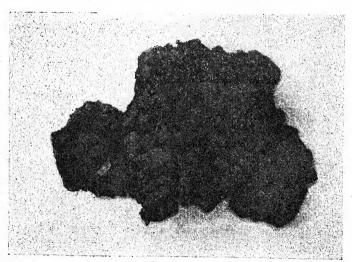


Fig. 2. Ustulina zonata. Photograph of a fructification of Ustulina zonata obtained from the base of a rubber tree.

rubber tree. Fig. 3 is a photograph of the base of a diseased rubber tree bearing a fructification (f) of *Ustulina zonata* at about soil level. The tree has been opened up in order to show the limits of diseased and healthy tissues (D and H respectively) above the collar.

DESCRIPTION OF THE FUNGUS.

In Malaya the fruit-bodies of the fungus arise as small greyish brown plates on the exposed lateral roots or collar of the affected tree, the growing margin of the fructifications being usually greenish in colour. Petch (4) describes the occurrence of a conidial stage when the fruit-body is young in which condition the surface is covered with a white felt consisting of slender, closely packed

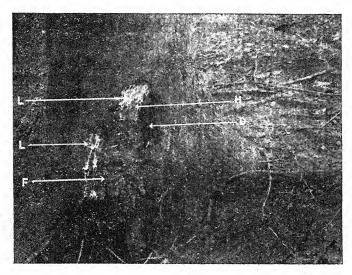


Fig. 3. Ustulina zonata. Photograph of the lower part of a diseased rubber tree bearing a fructification of U. zonata (F). The tree has been opened up to shew the limits of diseased and healthy tissues (D and H respectively) above the collar. Latex (L) has exuded where healthy bark has been cut.

conidiophores which abstrict small, hyaline spores from their extremities. I have not found this conidial stage on young fructifications kept under observation in Malaya, though it may be subsequently found. Mr. T. Petch has, however, kindly sent me some specimens in the conidial condition taken from a Mango tree in Ceylon, from which Fig. 4, A, has been drawn. The conidia are about $4\mu \times 2\mu$ in size. These fructifications in the conidial stage from Ceylon are much lighter in colour than the fructifications devoid of conidia of about the same age obtained in the Federated Malay States. Adult fruit-bodies gathered in Malaya have been compared with mature specimens of Ustulina zonata from Ceylon and other countries, in the herbaria at Kew, and at Peradeniya, with which they are undoubtedly identical, hence there is no hesitation in naming the fungus Ustulina zonata (Lev.) Sacc.

The plate-like fructifications of *Ustulina zonata* are several inches across when fully developed and are marked by an irregular and obscurely zoned surface, which is punctured by minute black dots scarcely visible to the naked eye. The outline of the fruit-body is irregular and the centre is often roughly corrugated. Petch (4) points out that the fungus is extremely variable, and says that the fructifications are sometimes stalked. The variation in the Malayan specimens is also a marked feature. If the grey brown surface of the fructification is scratched, a black layer is seen which is also exposed at times by the natural wearing away of the thin covering.

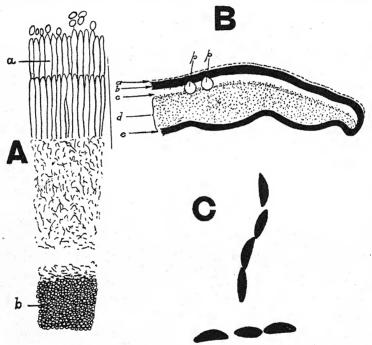


Fig. 4. Ustulina zonata. A. Section of the upper part of a fructification shewing the conidial stage (material sent from Ceylon), \times 630: a, conidiophores; b, portion of upper black layer. B. Diagram, about eight times natural size, of section of mature fructification; for explanation see Text. C. Mature ascospores, \times 330.

The fruit-bodies though rather soft when young are brittle when mature; they are about $\frac{1}{8}$ inch thick or rather less. Fig. 4, B, illustrates the different layers seen in section when a mature fructification is broken across. On the upper surface a represents the remains of the greyish brown film which, in the Malayan specimens so far examined, is sterile, but in the Ceylon specimens gives rise to the conidial stage; b is the upper black zone which

sometimes becomes exposed by the wearing away of the greyish brown film above; c is a white layer in which the globular perithecia (b) are formed; d is a broader band grey in colour and leathery in consistency; and e is the black zone on the under surface, which is continuous at the margin with the black zone towards the upper surface. The black zones are brittle. The perithecia (p) are globose and communicate with the exterior by exceedingly narrow channels. The minute black dots seen on the fructification after the superficial grey brown layer has been worn away, correspond to the ostioles of the perithecia. They are raised very slightly above the general level of the surface of the fruit-body and are formed before the perithecia are fully organised. Each ascus contains eight, black, spindle-shaped spores which are somewhat inequilateral (Fig. 4, C). The dimensions of these spores are $28-32\mu \times 7-10\mu$. There are large numbers of thread-like paraphyses between the The ripe spores exude from the perithecia under moist conditions. When a portion of a fructification is kept damp in a Petri dish, the spores are liberated and look like drops of ink spread over the surface. The ascus walls deliquesce before the extrusion of the spores from the perithecia as in other members of the Xylariaceæ to which the genus Ustulina belongs; this behaviour of the ascus walls is probably an important factor in bringing about the liberation of the spores.

The genus *Ustulina* is distinguished from other members of the Xylariaceæ which have flat fructifications, by the fact that the fruit-bodies are rather soft when young and are covered by an evanescent layer which often forms conidia before the elaboration of the perithecia below. In the closely allied fungus *Daldinia concentrica*, the superficial layer of the young fructifications does not always form conidia, so it is not remarkable to find that the formation of conidia by the corresponding layer in *Ustulina zonata* is not constant.

The species *Ustulina zonata* was first described under the name of *Sphæria zonata* by Léveillé (3) in 1845 from material obtained on palms in Java. It has since been placed in the genus *Ustulina* by Saccardo (7).

Effect of the Fungus on the Tissues of Hevea.

Wood and bark invaded by the fungus become discoloured, and near the margin of the affected tissues conspicuous black lines are often present, these being caused by the dense aggregation and darkening of the hyphæ in the cells of these regions. Smaller black zones sometimes occur as islands a little distance away from the longer lines. Fig. 1 shows a general view of one of these black lines in the wood, which are closely similar to the black zones in the fructifications, Fig. 5 shows a section through one of these black lines seen under the microscope. The brown tissues bordering these black lines contain hyaline hyphæ which are especially



Fig. 5. Ustulina zonata. Section of black zone in diseased wood of Hevea brasiliensis taken from the collar of an old tree. x 330.

abundant in the vessels. It is noteworthy that the black lines often occur just within the margin of the region penetrated by the hyphæ. One one occasion tyloses were found in vessels affected by the fungus, but the presence of these ingrowths does not occur regularly as in the tissues of *Hevea* invaded by *Corticium salmonicolor* as

described by Brooks and Sharples (1). These conspicuous black zones are caused by the fungus forming a kind of sclerotic plate in the tissues, the difference between this aggregation and a typical sclerotium being that the latter does not include within it portions of the tissues of the host. These black zones differ from rhizomorphic strands in the same respect. The fungus invades the tree either in the collar or in one of the roots from either of which it advances, spreading more rapidly in a longitudinal than in a lateral direction. In advanced stages of disease several of the laterals and the tap root may be dead and the fungus may have progressed two or three feet up the trunk of the tree. In the latter case boring beetles often attack the affected parts of the trunk, as also happens sometimes with trees affected by Sphærostilbe repens. The presence of black lines in the roots of tea attacked by Ustulina zonata is mentioned by Delacroix and Maublanc (2).

The presence of black lines in dead rubber wood must not, however, be considered a certain sign that Ustulina zonata is present, as several of the fungi belonging to the Xylariaceæ are of common occurrence as saprophytes on dead branches and roots of rubber trees, and two of these, Numnularia pithodes (B. and Br.) Petch, and a species of Xylaria, have been found by the writer to produce similar black lines in the wood. On one occasion this species of Xylaria was seen to affect living tissues of exposed Hevea roots which had been badly wounded some time previously, possibly through being knawed by animals. This fungus had entered the wounds, and after setting up decay had advanced into the living tissues to some extent, although no serious damage was being done. It is only when these black lines in the wood and bark are associated with an extensive affection of the collar and root system of the tree that Ustulina zonata should be suspected.

PURE CULTURES OF THE FUNGUS.

Pure cultures were established from the mycelium present in one of the black zones taken from the collar of an affected rubber tree. In order to do this, small portions of the black plate were cut out under sterile conditions and placed on blocks of Hevea wood in culture tubes. In a short time a greyish mycelium began to grow from the black mass and spread slowly over the block of wood. This mycelium was fine in texture, and remained closely adpressed to the wood. At a later stage the mycelium in contact with the wood became black, and, together with the mycelium in the super-

ficial layers of the wood, formed a continuous black crust similar to the black zones in the collar of a diseased tree. In some of the cultures a black line was formed in the wood block a little within the surface. Fig. 6 shews a section of one of these black zones in a block of wood on which the fungus grew in pure culture.

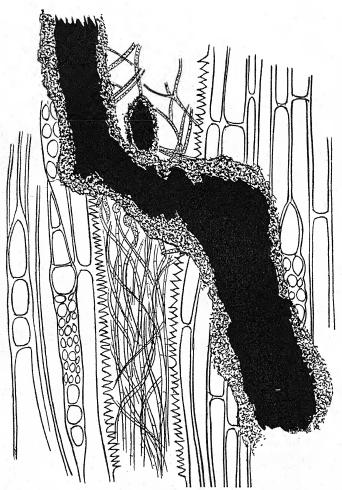


Fig. 6. Ustulina zonata. Section of black zone in wood of Hevea brasiliensis on which Ustulina zonata grew in pure culture. × 330.

Since returning to England I have found that the fungus grows well on sterilised blocks of Ash wood kept at a temperature of 25° C. At 12° C, however, it grows scarcely at all.

INOCULATION EXPERIMENTS.

After pure cultures of the fungus had been obtained, inoculation experiments were carried out upon seedling rubber plants growing in pots and upon trees about four years of age, situated on the slope of a hill. Blocks of wood on which the fungus was growing in pure culture were tied or placed against the main root of the seedling a little below the level of the soil. With the four-year-old trees either the main root or one of the larger laterals was inoculated in the same way. In three of the seedling plants thus inoculated the wood block bearing the fungus was placed against a wound made in the root with a scalpel; in three others the fungus was tied against the uninjured surface. A month later the leaves of one of the inoculated and unwounded plants began to droop, and, shortly after, investigation shewed that the plant was diseased at the collar, and there was clear indication that the fungus had spread from the wood block into the plant. Sections shewed a brown discolouration of the wood and bark of the root and collar above the place against which the wood block had been tied, but no black lines were present in the tissues. The pith was rotten for two inches upwards from the region of inoculation, and a hyaline mycelium was densely aggregated along the line of the cambium, where it formed a kind of pseudoparenchyma.

A week later, i.e., five weeks after inoculation, two other seedling plants, both of which had been wounded, began to droop, and examination shewed that they were affected in the same way as the seedling described above. The three other plants remained healthy. The third wounded plant, which did not become affected, shewed only a slight discolouration around the wound which was already partly healed over. Thus in this series of experiments, the fungus entered and successfully infected one unwounded plant and two wounded ones.

Of the fourteen four-year-old trees which were inoculated, eight were wounded before inoculation and six were not injured. The wounds made in these trees reached as far as the wood. Six weeks after inoculation the trees were examined, when it was found that the fungus had made considerable progress in each one of the wounded roots that had been inoculated, but, with one doubtful exception, had not penetrated the roots which had not been injured. The wood around the wounds through which the fungus had entered was markedly discoloured. Control wounds against which the fungus was not placed shewed much less discolouration in the

same period, hence the effect upon the inoculated tissues was not due to the entrance of other micro-organisms from the soil. The absence of infection in the uninjured roots of these four-year-old trees is certainly striking, although as described above, the fungus succeeded in invading the uninjured surface of the root of one of the seedling plants.

TREATMENT.

It has already been pointed out that in Malaya this disease chiefly affects old rubber trees. It is likely that the death of old plantation trees has often been attributed to Fomes semitostus (Fomes lignosus) when the loss was really caused by Ustulina zonata or by Sphærostilbe repens which also attacks mature trees more frequently than young ones. Fomes semitostus (Fomes lignosus) does not often attack old rubber trees partly because by the time a plantation is ten years old this fungus has generally worked itself out if the estate has received proper treatment. Fomes is the chief foe of young rubber, because it develops on jungle stumps soon after they begin to decay, whence it spreads to the roots of young rubber plants.

Petch (4) states that *Ustulina zonata* is the commonest root disease of tea in Ceylon, and says it is specially prevalent in plantations in which *Grevillea* or *Albizzia moluccana* has been cut down and the stumps left. *Ustulina zonata* grows on these dead stumps and, spreading along the lateral roots, comes in contact with the roots of tea bushes which are thus infected. The fructifications of this fungus are frequently found in Ceylon on dead stumps of *Grevillea* as well as around the collar of tea bushes.

Although fructifications of *Ustulina zonata* have not yet been found on old stumps in Malaya, it is likely that the fungus often begins to grow on decayed stumps from which it passes to the roots of rubber trees. On some of the older rubber estates on which the disease has been found, however, very few stumps remain and it is possible that there are other modes of infection. The fact that the collar and tap root are sometimes the first parts of the tree to be affected, points to the same conclusion. Several of the old trees seen to be affected by *Ustulina zonata* were previously attacked by white ants, and it is by no means impossible that the two attacks are connected in some way, possibly by the ants bringing the fungus into the tree. With *Fomes semitostus* (*Fomes lignosus*) there are good grounds for thinking that white ants frequently follow an attack by the fungus and it is possible that the reverse process

occurs in the case of *Ustulina zonata*. We have, however, much to learn yet about the methods by which root parasites enter their hosts.

The disease of the collar and root system of rubber trees caused by Ustulina zonata is by no means easy to distinguish in the early stages when there is some chance of dealing with it effectively, yet it is important that this should be attempted, as it is almost impossible to save the trees once the disease has made considerable progress. If the condition of the bark on one side of the collar of a tree arouses suspicion it should be examined and if found to be diseased all discoloured tissues should be cut out and burnt and the exposed surfaces tarred; diseased lateral roots should be destroyed, unless they are large when the unhealthy tissue should be excised. If the fungus has penetrated so far into the tree that it would fall if all the affected tissues were cut out, the tree is doomed and efforts to save it will probably be useless; since, however, the fungus spreads but slowly, the tree may be kept in tapping until the end. Such trees should be cut out when they cease to yield latex in paying quantities. Although no external mycelium has yet been found around trees affected by this disease, it would be acting on the safe side to isolate an infected area by means of a trench. The fungus probably spreads from one rubber tree to another chiefly by contact of diseased roots against healthy ones.

With the drastic thinning out which has been recently carried out on many estates and with the thinner planting of new areas than was formerly customary, it is important to remember that once the number of trees per acre falls below 80 to 100, the loss of a tree is a more serious matter than when an acre carried 150 to 200 trees. The smaller the number of trees remaining per acre the greater must be the attention paid in watching for the appearance of disease and treating it in the earliest stages, otherwise the yield from the estate will become seriously reduced. The disease caused by *Ustulina zonata* is a particularly insidious one, and rubber planters should be on their guard against it.

SUMMARY.

1. A disease of plantation rubber trees caused by *Ustulina* zonata and not hitherto recorded in Malaya is described. It is readily distinguishable from the root diseases caused by *Fomes semitostus* (Fomes lignosus), Sphærostilbe repens, and Hymenochæte noxia.

- 2. The disease chiefly affects the collar and root system of old rubber trees, though a few five-year-old trees have been attacked by it.
- 3. The fructifications of the fungus are greyish brown or blackish plates which are formed at the collar or on exposed lateral roots of diseased trees.
- 4. The fungus probably often begins to grow on decaying stumps though in several trees it has been found to follow attacks of white ants.
- 5. It is important that the disease should be dealt with in the early stages by cutting out and destroying all discoloured tissues.

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THE INTER-RELATIONSHIPS OF PROTISTA AND PRIMITIVE FUNGI.

By F. CAVERS.

(Continued from p. 104).

IV.—RELATIONSHIPS OF COLOURLESS FLAGELLATA TO INFUSORIA.

AS classified by Ehrenberg the Infusoria included Desmids, Diatoms, Bacteria, Sarcodina (excluding Foraminifera and Radiolaria) and Rotifers, as well as Flagellates and Infusoria as now recognised. Siebold (1845) narrowed the term to its present limits, except for the admission of some Flagellate families, and Bütschli limited the group by removing these families—Dinoflagellata (Peridiniales) and Cystoflagellata (Noctilucales)—to his Mastigophora (Flagellata). As now defined, the Infusoria are Protozoa in which the body is bounded by a permanent plasmatic pellicle and is therefore of definite form, never using pseudopodia for locomotion or ingestion; provided, at least in the young state, with numerous cilia or organs derived from cilia; and equipped with a double nuclear apparatus, as already stated.

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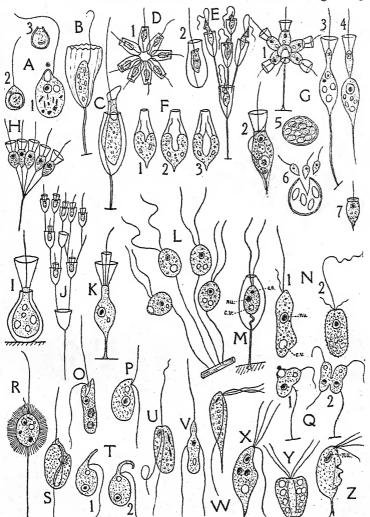


Fig. 2. Protomastigineæ. A, Oihomonas: 1, O. termo Ehrenb., about to ingest a food particle by means of a vacuole; 2, 3, formation of cyst in O. vulgaris Kent. B, Codonæca costata Clark. C, Bicæca lacustris Clark. D, Bicæca socialis Lauterb: 1, colony, 2; an individual of same. E, Poteriodendron petiolatum Stein, colony. F, Codonosiga pulcherrima Clark: three stages in division. G, Codonosiga botrytis Stein: 1, colony; 2, individual cell; 3, 4, two stages in transverse division; 5, cyst; 6, cyst breaking open and setting free young individuals; 7, young form showing beginning of peristome. H, Codonocladium umbellatum Tatem, colony. I, Salþingæca amphoridium Clark, a solitary form with theca and peristome. J, Polyæca dichotoma Kent, colony. K, Diplosiga frequentissima Zach., with double peristome. L, Amphimonas globosa Kent, four sessile individuals. M, Diplomita socialis Kent. N, Monas: 1, M. (Sterrimonas) formicina Kent; 2, M. vivipara Ehrenb. O, Physomonas vestita Stokes. P, Bodo edax Klebs. Q, Pleuromonas jaculans Perty: 1, shows ingestion of a food particle; 2 shows division. R, Phylomitus amylophagus Klebs, with two ingested starch-grains. S, Colponema loxodes Stein. T, Rhynchomonas nasuta Klebs, showing the motile proboscis-like appendage (straight in 1, recurved in 2). U, Elvirea cionæ Parona. V, Dallingeria drysdali Kent. W, Trichomastix lacertæ Blochm. X, Tetramitus dessissus Perty. Y, Collodictyon triciliatum Carter. Z, Trichomonas vaginalis Donné. Lettering:— c.v., contractile vacuole; e.s., eye-spot; nu., nucleus.

If stress is laid upon the dual character of the nuclear apparatus —as is done, for instance, by Hickson (1903) who sharply separates the Infusoria from the remaining Protozoa under the name Heterokarvota-then two groups of mouthless parasitic forms must be excluded. These groups are the Trichonymphidæ and the Opalinidæ: the former are uninucleate, while the latter have numerous small uniform nuclei and produce uninucleate gametes. These two families are united by Hartog into the group "Pseudociliata" and placed in the Flagellata; Delage and Herouard place Trichonymphidæ in the Flagellata, but the Opalinide are usually retained in the Infusoria. Bütschli (1887-9) regarded the Trichonymphidæ as an isolated and independent group derived from Flagellata. Senn (1900) calls attention to a number of organisms which in addition to typical flagella bear short cilium-like appendages, and suggests that these may form a transition between Protomastigineæ and the Ciliate Infusoria. Unfortunately these forms are still very imperfectly known, little or nothing being available regarding their life histories.

Excluding the Opalinidæ, which are probably heterokaryote and therefore true Infusoria, we may bring together here a number of forms which may be regarded as transitional between Flagellata and Ciliate Infusoria, and which might be called "Cilioflagellata." These forms may be placed close to the Pantostomatineæ, from which they may be suppossed to have arisen, and they may perhaps be considered as a group only little less generalised than the Pantostomatineæ themselves, and as having given rise to the remaining colourless Flagellata (Distomatineæ and Protomastigineæ) as well as to the Infusoria. Some of the types of "Cilioflagellates" are represented in Fig. 3. In Trichonympha the whole body, which is divided by a constriction into a shorter conical anterior region and a longer and wider ovoid posterior region, is covered with long flagella: in Leidyonella the flagella are also numerous but restricted to an anterior and a posterior tuft; in Lophomonas they are limited to the truncate and hoof-shaped anterior end of the body; in Spironema they are fewer and arranged in two lateral groups of about six on each side of the anterior pole; in Trichonema there is a single long anterior flagellum, with numerous much shorter cilium-like appendages either covering the whole of the body (T. gracile) or the posterior half (T. hirsutum); Mitophora is like Trichonema except that the "cilia" are apparently disposed in a single line running nearly the whole length of the body; in Heteromastix there are two anterior flagella and a line of "cilia" running along about half of one side of the body; in Stephanomonas the truncate and concave anterior region (mouth-spot?) bears a long central flagellum and a marginal circlet of "cilia"; in Pyrsonympha, a parasite, the anterior flagellum serve for attachment to the tissue of the host, while the "cilia" are few and in scattered patches, while in Dinennymbha the whole of the spirally coiled body is clad with "cilia" and there is no flagellum though the cilia at the anterior end of the body are somewhat longer than elsewhere.

Though practically nothing is known about the genera just mentioned excepting their body-form and the general character of their appendages, it would seem that we have here forms showing a transition from flagella to cilia, or a series of generalised types

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possessing both kinds of appendage. Such forms may be regarded as giving rise to the Infusoria; indeed the only changes required in order to obtain a typical simple Ciliate from such a form as, say, Trichonema gracile would be the loss of the flagellum, the specialisation of the nuclear apparatus and the acquisition of an oral groove or mouth-spot. A mouth-spot is apparently present in some of these "Cilioflagellates"—e.g. Stephanomonas, and possibly Lophomonas and Spironema also; Dinennympha has lost the anterior flagellum;

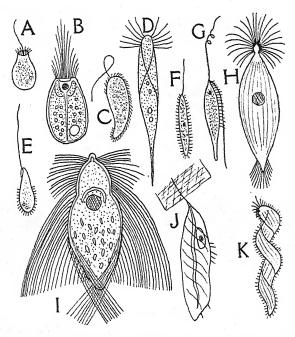


Fig. 3. Forms possibly Transitional Between Flagellata and Infusoria. A, Stephanomonas locellus Kent. B, Lophomonas blattarum Stein. C, Mitophora dubia Perty. D, Spironema multiciliatum Klebs. E, Trichonema hirsulum From. F, Trichonema gracile Moeb. G, Heteromastix proteiformis Clark. H, Leidyonella cordubensis Frenz. I, Trichonympha agilis Leidy. J, Pyrsonympha vertens Leidy. K, Dinennympha gracilis Leidy.

while the fact that the dual nuclear apparatus character has apparently arisen independently in the two distinct offshoots of the Protomastigineæ which are classed together under the heading of Trypanosomes—though the Trypanosome nuclear apparatus is not, it must be admitted, heterokaryote in the same sense as the Infusoria—reduces the difficulty presented by this very characteristic feature of the Infusoria. That the trichocysts or stinging capsules so common in Infusoria have arisen more than once in the evolution of Protista is indicated by the presence of these structures in some Peridiniales and allied Flagellata (Pouchetia, Polykrikos).

V.—THE PROTEOMYXA.

Zopf (1885 a) divided the Mycetozoa, regarded in a wide sense, into two main groups-the Monadineæ (mostly aquatic, often parasitic, usually producing zoocysts, i.e., cysts whose contents were set free as flagellate or amæboid spores, plasmodium formation absent or slight) and Eumycetozoa (aerial, never parasitic, without zoocysts, plasmodium formation invariable and usually striking. He divided the Monadineæ into two series-Zoosporeæ (zoocysts producing flagellulæ, i.e., flagellate spores) and Azoosporeæ (zoocyst producing amœbulæ, i.e., amœboid spores). The name Proteomyxa was proposed simultaneously by Lankester (1885) for a group which practically coincides with Zopf's Monadineæ. As defined by Lankester, the Proteomyxa include those forms of the Sarcodina division of Protozoa in which the pseudopodia are usually granular, fine, flexible, and not freely branched; in which reproduction may take place by simple fission but more usually by multiple fission in a brood-cyst; in which plasmodium formation occasionally occurs but never leads to the production of a massive fructification; and in which encystment (or at any rate a resting stage at maturity) is a characteristic feature. Zopf, Lankester, and the majority of zoological writers include in the group, now generally known by the latter's name Proteomyxa, the parasitic forms which are now placed in the Plasmodiophoraceæ (Phytomyxineæ) division of Mycetozoa. The group has undergone vicissitudes in successive schemes of classification of the Protozoa, but there seems to be general agreement among zoologists that it is a highly artificial one, though convenient as a "lumber-room" for a number of forms which are difficult to place in any of the other groups of Protozoa without enlarging and rendering vague the definitions hitherto applied to these groups.

(To be continued).

ERRATA.

THE AUSTRALIAN MEETING OF THE BRITISH ASSOCIATION.

1. THE BOTANICAL EXCURSIONS.

By E. R. SAUNDERS.

Vol. XIV, Nos. 2 and 3.

p. 53, line 26, for Mr. E. C. Andrews read Mr. C. Andrews.

p. 54, line 25, omit quercifolia after the name Thomasia.

NEW PHYTOLOGIST.

Vor.. XIV, Nos. 6 & 7.

JUNE & JULY, 1915.

[Published August 4th, 1915].

PLEODORINA ILLINOIENSIS1 KOFOID IN BRITAIN.

By W. B. GROVE, M.A.

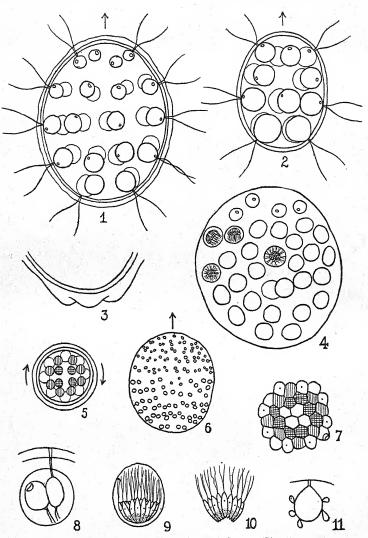
[WITH ELEVEN FIGURES IN THE TEXT].

MIOWARDS the end of March, 1915, I made a very large gathering of this species, from cart-ruts in a ploughed field at Harborne, near Birmingham; the water was covered at the time by a coat of ice. The gathering was almost pure, only a Pandorina or two and a few Flagellates being mixed with the predominant species. This, as will be seen later, is an unusual circumstance: Pleodorina has been almost always found accompanied by Eudorina but none of the latter occurred in the Harborne material until nearly the end of April, when a small number began to be found in the field. When brought home, the gathering was preserved, and flourished in a basin in a cool room for more than seven weeks; at the same time the species increased enormously in its original habitat and was kept under observation till the ruts dried up towards the end of May; during the latter part of the time a number of Rotifers and Anthophysa vegetans, etc., made their appearance as well as the Eudorina.

All the colonies of the *Pleodorina*, without exception, were ellipsoidal in shape (Fig. 1), the diameters being occasionally in the ratio of as much as 10:7, though more usually about 9:7 and, although many individuals had the diameters more nearly approaching equality (as near as 6:5), none were seen that appeared circular, out of the immense number examined, except of course in end view.

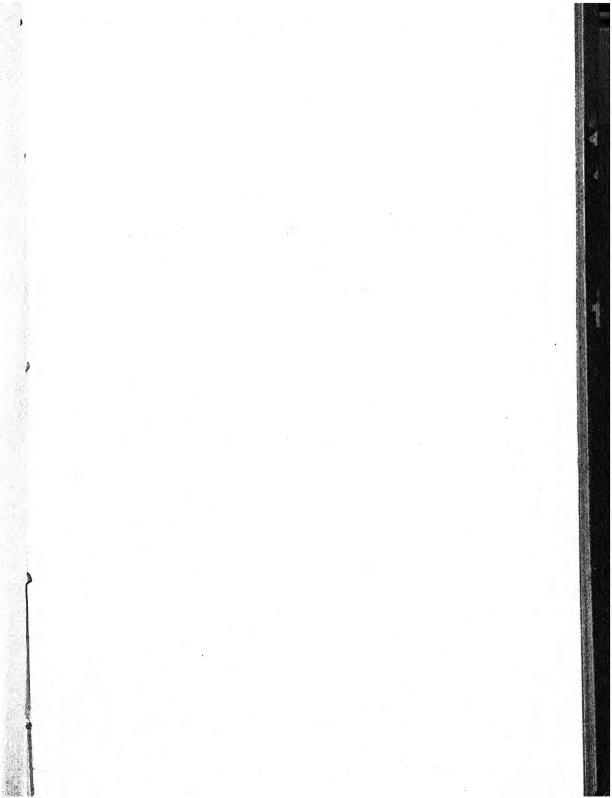
Observation soon showed that these colonies possessed a very marked polarity, always advancing in the direction of the longer axis, with one particular end foremost, rotating at the same time about that axis so that, when viewed from the anterior end, the

¹ Kofoid wrote "illinoisensis" which is repugnant to the Latin method. The law of priority does not concern itself with grammatical errors.

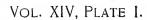


Figs. 1-11. Pleodorina illinoiensis (except Fig. 6).

- Fig. 1. Mature comobium, × 360.
- Fig. 2. Mature 16-celled comobium, x 360.
- Fig. 3. A mamillated posterior end, x 360.
- Fig. 5. Mature antheridial colony; the gelatine is much softened and the antherozoid-plaques are ready to escape. The four anterior cells are undivided (only four antheridia are filled in, the remaining 24 are similar) \times 180.
- Fig. 5. A comobium, viewed from the anterior end; the arrows show the direction of rotation. (Somewhat diagrammatic).
 - Pig. 6. Pleodorina californica, from a mounted specimen (California), x 180.
- Fig. 7. A 32-celled plakea seen in plan. The four unmarked cells in the centre will be the anterior cells of the phialea; the unmarked ones at the



THE NEW PHYTOLOGIST.

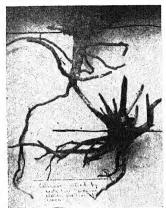




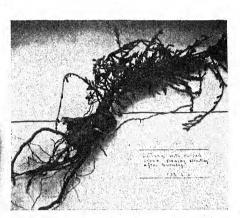
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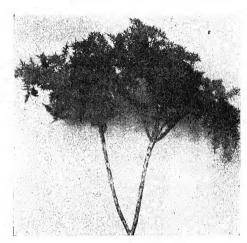
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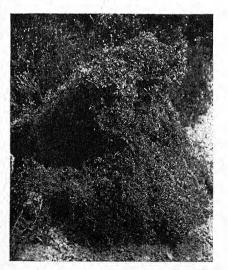
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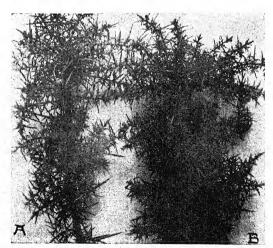
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Phot. 5.



Phot. 6.



Phot. 7.

FRITSCH & SALISBURY.—HEATH ASSOCIATION, HINDHEAD COMMON.

Fig. 8. A cell from an antheridial colony, which has just undergone the first division towards forming antherozoids, \times 600.

Fig. 9. Antheridium with mature antherozoids, x 600.

Fig. 10. Free antherozoid plaque, in optical median section, x 600.

Fig. II. Presumed young oospore, showing expressed oil-drops, x 360.

cells moved like the hands of a clock from left to right (Fig. 5); only very rarely (and always when checked by some obstacle and for a very short time) did any of the maturer colonies vary the rotation into the opposite direction. Young colonies, while still in the gelatinous matrix, a considerable time before emergence, would sometimes begin to rotate slowly and with jerks and wriggles, but still on the whole in the clockwise direction. It was interesting to observe the free colonies, when enmeshed among a few loose fibres of cotton wool (which kept off the pressure of the cover-glass), "nosing" slowly round the borders of the lakelet in which they were imprisoned, like an intelligent dog, passing into every bay and inlet as if trying to find a way of exit, and always keeping the same end foremost except when backing out of a narrow gulf in which there was not room to turn.

The colonies, when mature, measured about 150-200 u in length: they consisted of 32 cells, arranged in five distinct bands or zones, the anterior and posterior ones containing each four cells, and the intermediate ones eight each (Fig. 1). Rarely a colony with four zones of only four each was to be seen (Fig. 2). The origin of these will be shown later. Each colony was surrounded by (usually) two mucous coats of different densities; the inner denser one had a very regular ellipsoidal outline, both without and within, while the outer coat was somewhat irregular in thickness and sometimes wanting. The matrix, in which the cells were embedded, within the inner coat, was also gelatinous but less firm in texture. The different layers. which varied much according to age, could be seen with great distinctness when the living colony was heavily stained with diamant-fuchsin; this stained the inner coat most deeply, and also the flagella which were thereby rendered very conspicuous. Delafield's hæmatoxylin and other reagents were less effective. I could not succeed in demonstrating any hexagonal reticulations round the cells with the methylene-blue which Kofoid recommends for the purpose, until I adopted the expedient of pressing upon the cover-glass so as to expel the cells; then five rows of faintly outlined irregular hexagons could sometimes be detected. But this was an artefact, produced by the mutual pressure of the gelatinous capsules surrounding each cell at a certain stage. There are no cell connections in Pleodorina and no contiguous polygonal compartments such as Volvox possesses.

The outer coat frequently showed slight irregular projections at the posterior end, which occasionally assumed the form of three regular mamelons placed at the corners of a triangle (Fig. 3). When they occurred, these mamillæ were rendered more conspicuous by a number of minute highly refringent colourless granules, attached to them as well as to the rest of the outer surface: these granules might be nothing but particles of débris adhering to the mucus. although they seemed to be too regular in size for such a description -weak acids had no effect upon them.

The most striking point about the colonies was the inequality in size of the cells of which they were composed, the four anterior cells being always distinctly smaller than the others (Figs. 1, 2): in many cases, but not in all, it could be seen that the four posterior cells were also larger than those in the intermediate zones. The ratio of the diameters of the smallest and largest in a colony varied from an average of about 1:11 to 1:2 in the few extreme cases. There was oftentimes, in addition, a certain wider spacing apart of the front rows which caused the anterior half of the colony to show decidedly more of the hyaline mucus than the posterior half. The measurement of the cells in one individual gave such sizes as, e.g., 25, 24, 22, 21 and 17μ , or 18, 15, 14, 13.5, 12.5μ , taking the rows respectively from back to front, although the decrease was not always so regular.

Each cell was approximately spherical, containing a hollow cup-shaped chloroplast, with a nucleus occupying nearly the whole of its central cavity and a conspicuous nucleolus; the anterior portion of the protoplasm was hyaline and bore at its upper end (not infrequently on a short projecting neck) two flagella of the usual kind. The chloroplast contained, in the mature cell, from one to eleven (most often three or four) roundish pyrenoids, but no pyrenoid could be detected in the cells of the very young daughtercolonies.

Another striking feature of the colony related to the red evespots situated near the base of the flagella. considerably in size, being largest (3μ) in the four anterior cells, and thence diminishing gradually in each zone, until in the posterior cells they were minute or even completely absent (Pig. 1). Their

colour was very brilliant; each eye-spot was circular in face-view, but subreniform or lunate (i.e., really basin-shaped), with the concavity directed outwards, in profile; it would act like a concavo-convex lens. In the anterior cells the two ends of the crescent frequently protruded the cell-wall beyond the limit of the circular cell-outline.

The colonies were multiplying rapidly at the time of gathering and continued to do so in the basin in which they were kept; the divisions took place chiefly in the night and forenoon. The process was as described by Conrad for Eudorina elegans, except as to the last two states, G and H in his Fig. 9 (6, p. 334); for these the figure given here (Fig. 7) should be substituted. From the fourcelled stage onwards the disc formed by the dividing cells is seen to be hollowed like a saucer, with the concavity directed outwards; this is called the plakea stage. Then the four corners rise up and meet in the 32-celled stage at a point above the centre of the plakea and at some distance from it, while the intervening cells arrange themselves in three alternating rows, as shown in Fig. 1, round the circumference of the ellipsoid.

A hollow structure formed in this way is called a *phialea*; the centre of the plakea becomes the anterior pole, the opposite pole where the corner cells are united by mucus is called the *phialopore*. The globular or ellipsoidal colonies of *Volvox* are formed in a similar way, and it has been stated that in that genus the extrusion of the daughter-colonies always takes place by the rupture of the phialopore; that may or may not be true, but it is certainly not so in the present species.

When the phialea is first formed, the cells, which measure about 4μ , are in close contact and are all alike except one. For, as the division takes place, the original eye-spot remains unchanged and becomes a part of the cell in which it happens to lie; but since it is always on the outside edge of the mother-cell, it finally (while still bright red) comes to lie in one, the first (Fig. 7) or more commonly the second, of the cells forming an outer edge of the plakea, i.e., usually in the first or second (or rarely in the third) zone of the phialea, counting from the phialopore. No other eye-spots could be detected in the just-formed phialea; these like the pyrenoids appear to be formed de novo, while the original eye-spot disappears, first losing its brilliance (though not its size) and becoming yellowish-red. The minute new eye-spots also seemed at first to be yellowish and more like an oil-drop; they did not assume the

bright-red colour until the colony was nearly ready to start off on its own career. It was not found possible to see the two eye-spots (the old and the new one) at the same time in the same cell, probably because the old eye-spot is necessarily in one of the posterior cells in which the new eye-spots are often absent or imperceptible.

That eye-spots are really organs for the perception of light cannot be doubted. The presence of the largest eye-spots in the anterior cells and their regular diminution in size from front to rear are closely correlated with the definite forward motion. The young colonies, in which eye-spots are only beginning to be developed, are less decided in the direction of their movements than are the mature colonies.

What has been described applies to the 28 cells not in the anterior row; the process of division was more or less simultaneous in them, although it always began in the posterior part of the colony and the more posterior cells usually completed it before the less posterior.

In a very large proportion of cases the four smaller anterior cells underwent no division at all; sometimes they began when the others had nearly completed the process, but in the majority of these instances they advanced only to the 16-celled plakea, of which the corners then rose up and formed a 16-celled phialea considerably smaller than the others in the same group. This was the way in which the 16-celled colonies (Fig. 2), occasionally to be seen swimming about, chiefly arose. Very rarely all the cells seemed to divide alike and more or less simultaneously.

It was in these smaller colonies that the behaviour of the original eye-spot was most plainly to be seen. Since the cells from which they were formed had the largest eye-spots, when the 16-celled plakea was completed the eye-spot occupied a large fraction of the cell in which it lay, and it was equally conspicuous when the phialea was first formed; yet, when these colonies became free and were on the point of swimming about, no eye-spots or only very minute ones (as the case might be) could ever be detected in them.

The liberation of the daughter-colonies, which at that time measure about $35 \times 27\mu$, from the mother takes place in *Pleodorina* exactly as it is known to do in *Eudorina* and *Pandorina*, by a slow dissolution of the mucous envelope. When first released, there is no essential difference between those of *Pleodorina* and of *Eudorina*. In no case was there ever seen an extrusion of the

daughter-colonies at the phialopore. The manuelons which Kofoid found there he regarded as possibly the points of exit; but that this is untrue is shown by the fact that they could be seen in perfection in many colonies in which division of the cells had not even begun.

When the first gathering was made, a number of plakeas of cells were seen swimming about in a way resembling that of a fly buzzing on a window pane. There were about 64 cells in each (58 were counted in one instance), but they were so crowded that it was not easy to be sure of the number. The cells were more or less pyriform with the narrow ends all directed to one side, on which also lay all the cilia. These were at once interpreted as microgametes (antherozoids), but none were seen in situ and for a long time no more could be found. Then the expedient was adopted of letting a little water containing a few thousands of the colonies nearly dry up; on moistening this again it was found to comprise numerous colonies which had produced microgametes. But the greatest number were found in a mass of the alga which had been kept crowded for some days in distilled water in a beaker, and amongst these numerous free antherozoid-groups were also seen buzzing about in their characteristic way. The colonies of antherozoids were easily distinguishable under a low power by their pale colour; most of them had had 32 and a few 16 cells, and in many of these some of the cells still remained undivided. Very frequently the four anterior cells were unchanged, while among the rest of the cells 1 to 6 might also still remain undivided, though in the majority of cases all the 28 cells, or even rarely all the 32, had formed groups of antherozoids (Fig. 4).

In certain cases fully-formed ordinary comobia occurred mixed with the antheridia in the same colony. The table given over page summarises the particulars of a few of these, but they were not numerous; only those in which the antheridia and comobia seemed ready to escape were reckoned.

Each microgamete was about $12-15\mu$ long, had an elongated fusiform but changeable shape, was pale-greenish at the posterior end and uncoloured in the anterior half, where a minute but bright red eye-spot was situated just in advance of the middle; it had two flagella of rather more than its own length at the forward end.

The microgametes were seen in profile to be arranged more or less parallel to one another in a dense bundle (Fig. 9), with the ciliated ends usually directed towards the centre of the colony, and in plan 32 could be seen placed exactly as in the 32-celled plakea of

the vegetative division (see Fig. 7). The cell-division in the formation of the antherozoids is the same in detail as in the formation of daughter-cœnobia, but the former can be carried a step farther, and differs, moreover, in the fact that the cells put out flagella at an early stage. Comparatively few bundles of 64 antherozoids, such as were seen at first, could be found on the later occasions. When the group of microgametes was formed from any one of the cells in the anterior half, the large original eye-spot could always be seen (still retaining its red colour) outside the group towards its base; rarely the two flagella belonging to the mother-cell of the group also remained unchanged outside the mucus.

COLONY	Anterior Zone.	Second Zone.	THIRD ZONE.	FOURTH ZONE.	Posterior Zone.
1	4 undivided	4 antheridia 4 cœnobia	8 cœnobia	8 cœnobia	4 cœnobia
2	2 two-celled 2 four-celled plakeas	5 antheridia 3 cœnobia	8 cœnobia	8 cœnobia	4 cœnobia
3	4 eight-celled plakeas	8 antheridia	6 antheridia 2 cœnobia	4 antheridia 4 cœnobia	4 cœnobia
4	1 two-celled 1 four-celled 2 eight-celled plakeas	8 antheridia	7 antheridia 1 cœnobium	6 antheridia 2 cœnobia	2 antheridia 2 cœnobia
5	2 four celled 1 eight-celled 1 sixteen- celled plakeas	13 antheridia and 3 cœnobia, the rest having escaped			

Since division always begins in the posterior end, it will be seen that (when antheridia and comobia both occurred) the antheridia were the later formations.

The period during which the antheridia occurred lasted about a fortnight; after that no more were found in the cultures, although further attempts at starvation were made. The statement made by Merton that the flagella of the mother-cell and its eye-spot always remain attached to the same daughter-cell is not correct with respect to either the antheridial or the vegetative divisions. On one occasion, in a young antheridial colony, a two-celled stage was found in which the beginnings of two flagella could be seen on the inner side of

each cell, the two old flagella being attached on the outer side to one of the cells and the large eye-spot being in the other (Fig. 8). Other similar cases were seen in a fresh outburst of antheridia which occurred in the field at the beginning of May.

The antherozoid-groups escape whole from the softening mucus of the mother-colony; while trying to free themselves, they have a different motion from that of the daughter-cœnobia. They rotate and oscillate slowly, first in one direction, then in the opposite; during this time their flagella frequently look knobbed and have been so described, but more careful observation shows that this appearance is due to a rhythmical undulation passing along them, from base to apex, in the line of sight. When swimming free the groups are not surrounded by a mucous envelope (Fig. 10). After buzzing around some of the other colonies for a considerable time, presumably in search of a colony containing megagametes, they become dissociated into their constituents.

A small number of colonies showed a slight modification of the ordinary form of cell, which seemed to indicate them as female colonies. The presumed megagametes (never in the anterior zone) were slightly larger and darker in colour and, though no fertilisation was detected, some of them were seen surrounded by a thicker smooth wall and containing a quantity of oil which was expelled from them by pressure (Fig. 11). These were most probably the young oöspores; the colonies in which they occurred had the mucus much swollen, just as in the mature antheridial colonies.

In considering what rank shall be assigned to these organisms, we meet with a very curious and involved state of things. The form of Eudorina elegans with which British microscopists are familiar is invariably described as globular, and the 32 cells are all alike in size, but in the mature colonies the eye-spots are largest in the foremost cells and become minute or non-existent in the posterior row, though the descriptions in British works do not mention this fact. Moreover mamelons at the posterior end seem not to have been observed. Nevertheless ellipsoidal colonies of Eudorina do occur in Britain, though the cells remain all alike in size; most of the mature ellipsoidal colonies which I saw were smaller than those of the Pleodorina.

On the Continent, Eudorina is described as being ellipsoidal or sub-globular, never really spherical, and posterior mamelons are found in many cases. Conrad (6) describes the cells as alike in size in the same colony, ranging from 4μ when young to 25μ when adult.

The young colonies measure $55 \times 45\mu$, the mature ones $170 \times 140\mu$; they consist of 32, rarely of 16 cells, arranged in five or four distinct zones respectively.

Professor Henfrey described in 1856 (8), from a pond in Middlesex, what he called, (probably on account of its shape) Pandorina Morum, but the shape of the cells in his figures makes it clear that he had before him Eudorina. The colonies were ellipsoidal, the diameters being about as 9 or 10:7; no posterior mamillations are shown. The globose cells are figured as all alike in size in each colony, but in other respects, in shape and zonal arrangement, they resembled the Harborne specimens.

In 1857, Carter (1) found in tanks at Bombay, in May and June when they were nearly dried up, a quantity of Eudorina elegans of a distinctly ellipsoidal shape; each colony had 16 or 32 similar cells. and many were mamillated at the posterior end; they varied from 25 to 140µ long according to age, and always swam with one end foremost, rotating as frequently in one direction as in the other. largest eye-spots were in the anterior cells. In the 32-celled stage, in certain cases, he found the four anterior cells to divide into 64 pyriform antherozoids with a mass of cilia turned to one side, the two original flagella and the original large eye-spot still persisting. The remaining 28 cells of the colony he regarded as female cells. and he considered that fertilisation took place within the colony, the antherozoids becoming dissociated and swimming about singly within its gelatinous envelope. The antherozoids and oöspheres resembled those described above, except that the former are stated to be colourless at both ends, and faintly green in the middle. The actual fertilisation was not seen, and these observations have never been confirmed.

In 1894, Shaw described (14) a new genus Pleodorina, agreeing in most respects with Eudorina but having cells of two types, "vegetative" and "gonidial," situated respectively in the anterior and posterior parts of the colony. He assigned to it a species, P. californica, in which the number of cells is given as 128 (rarely 64) the vegetative cells constituting approximately the anterior half of the colony (Fig. 6). The cells were all alike at first escape, but when mature the gonidial cells measured 2-3 times the diameter of the vegetative cells. The maximum diameter of a colony is stated to be 175-300 μ , and the colonies, which revolved clockwise, were globular or broadly ellipsoidal. This species, originally found in California, has since been discovered in Illinois and Indiana, and

in other parts of the American continent, as well as in Europe, Java and Ceylon: see below.

In 1898, Kofoid described (10) an alga, chiefly from a flooded area on the banks of the River Illinois, to which he gave the name Pleodorina illinoisensis. It was associated with Eudorina elegans and Pandorina Morum, as well as with many other plankton organisms, animal and vegetable, in shallow warm water. The colonies were ellipsoidal, consisting mainly of 32 cells, rarely of 16, still more rarely of 64. The shape was quite constant, the average size of the mature colony being $113 \times 94\mu$; the youngest colonies on escaping, measured about $46 \times 38\mu$, the largest were $200 \times 175\mu$. The young cells varied in the earliest phialea stage from 3.5 to 5μ , the vegetative cells from 9.5 to 16.8 \mu, the gonidial cells from 15 to 25μ; they were all spherical and arranged in the usual zones. Each colony had both types of cells, the vegetative being the four anterior ones; the diameters were usually in the ratio of 1:13, and the largest and smallest of each kind were much the same as in the Harborne specimens. The gelatinous envelope had two layers and was often provided with protuberances at the posterior end (three are shown in pl. 34, Fig. 4) which Kofoid suggested to be the places of exit of the daughter-colonies. He observed similar protuberances on the Eudorina and Pandorina in the same material, but did not observe the escape of any of the daughter-colonies. In the Harborne material, as already stated, nothing was seen to bear out Kofoid's suggestion. The eye-spots, Kofoid says, decreased in size from front to rear, but apparently all the "gonidial" cells (excluding the dead ones which were to be met with from time to time) were regarded as being of the same size. The rotation of the colonies took place in either direction, though "right over to left" is said to have preponderated.1 The four anterior cells Kofoid considered to be almost purely "somatic"; in two cases, he says, they had degenerated, but in one case they had begun to divide, one of them being as yet undivided and the three others being in the two-celled stage. Further, in two instances Kofoid saw mature colonies in which four daughter-colonies smaller than the rest (and of 8 and 16 cells respectively) were present "at one pole," he does not say which. This account reads as if paucity of living material or insufficient length of observation makes the conclusions uncertain. They agree exactly so far as they go with my results, but they rest

¹ Unless the observations are made under a high power, it is quite easy to imagine a change of rotation as the upper or lower surface comes into focus.

upon too narrow a basis; a longer study would probably have revealed a greater variety of states. Unfortunately, however, Kofoid says, the species entirely disappeared after eleven days (June 16-27), a kind of disappointment from which many an algologist has similarly suffered.

In July, 1903, Merton (11) found P. illinoiensis in Germany at Heidelberg and also received it in 1907 from the Bavarian Palatinate; it was accompanied by Eudorina and Pandorina. In the year 1907, it began to appear, he says, in the latter half of June increasing during July, towards the end of which month he found for the first time the sexual stages; eight days later it had all disappeared. The colonies were all larger than those of the Eudorina; each consisted of 32 cells, the vegetative cells measuring $11-12\mu$, the gonidial cells $19-21\mu$. The megagametes were a little larger; the microgametes formed plakeas of 64 or 128 cells; the zygotes had a rather thick smooth membrane and finally a yellow-brown colour.

Pritsch in 1904 (7) found P. californica in tanks in Ceylon, associated with a form which could not be distinguished from Eudorina elegans.

In 1905, W. West and G. S. West (16, p. 506, pl. 6, f. 14), recorded *Pleodorina californica* from a lake in Lewis, Outer Hebrides. The colonies occurred among ordinary globular *Eudorina elegans*; they were broadly ellipsoidal with slight posterior lobes, but had only 32 cells, about half of them being vegetative: thus agreeing with neither of the described species of *Pleodorina*, but sharing the characters of both. The vegetative cells measured 6.5-7.5 μ , the gonidial cells 13.4-16.5, *i.e.*, in a ratio of about 1:2. It is plausibly suggested (*l.c.*, p. 507) that these individuals were only *Pleodorina*-states of the *Eudorina*.

Again, in 1906, the same authors found in a lake in Galway (17, p. 134, pl. 10, Figs. 7-8), among an immense number of ordinary Endorina, two interesting colonies which differed from the rest. They were still gobular, but small and large living cells (diameters about as $1:2\frac{1}{2}$) were indiscriminately mixed, with a few disintegrated dead cells scattered among them in one case. The authors considered these colonies to be mere states of the Endorina.

At the end of April, 1911, Chatton (3) discovered *Pleodorina* californica in a little pool in the south of France. It was accompanied as usual, by *Eudorina* and *Pandorina*, and disappeared at the beginning of July. The rotation was always clockwise. He observed for the first time the sexual reproduction, which continued only for a

few days. The microgametes were about 20μ long; they penetrated into the female colony, but the fertilisation was not seen. The megagamete surrounded itself with a membrane. Misled by a superficial resemblance, the author compares the phialea to the blastula of an animal organism, as does Janet (9) in Volvox.

It is evident from the above that the Harborne specimens are identical with Kofoid's *P. illinoiensis*. If it had been permissible to select features from, say, two colonies and combine them into a single figure, an almost exact parallel to Kofoid's figure might have been obtained. This species has been previously found in Britain in a pond on Skipwith Common, North Yorkshire, and in several places in Scotland. For this information and the opportunity of examining the Skipwith specimens, which are identical with mine except in the absence of the posterior mamelons, I am indebted to Professor G. S. West, who has also given me help in connection with the literature of the subject, and in lending a mounted specimen of *Pleodorina californica*.

But it is plain, on considering the whole matter, that the distinction between Pleodorina and Eudorina is a somewhat slender one, so far as it relates to the difference in shape of the colonies and in size among the cells in the same colony. The additional distinction alleged in the original diagnosis, viz., the occurrence of two types of cells in Pleodorina, gonidial and vegetative, is seen to be not absolute, but only relative; the vegetative cells in P. illinoiensis can divide, but usually do so less frequently and at a later period than the gonidial cells. Instead of regarding Pleodorina as a distinct genus, we might speak, as even Kofoid suspected, rather of a Pleodorina-state of Eudorina, though it is not clear what causes the latter to assume that state in preference to the normal form. The four anterior cells, which evidently possess the greater command over the movements of the conobium, may be regarded as giving up in part their function of reproduction, in order better to fulfil the Thus, as has been often stated, Pleodorina is an former rôle. advance on Eudorina in the direction of Volvox, where the distinction between somatic and reproductive cells is strongly accentuated. But the first-named genus seems to be still in a state of flux, so that varying evolutionary stages between it and Eudorina can at times be met with. However, many phanerogamic genera rest upon no better basis, therefore, for the sake of convenience, Pleodorina should still be maintained until the facts are better known.

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ADDITIONAL NOTES ON MARINE PYRENOMYCETES.

By Geo. K. Sutherland.

[WITH THREE FIGURES IN THE TEXT].

ORCADIA PELVETIANA NOV. SP. (Fig. I, 1-4).

YCELIUM in quibusdam locis, hyalinum; stroma nulla; perithecia simplicia, $110\text{-}140\mu$ diam., globosa, mollia, pallida, thallo omnino immersa, ostiolo longissimo, $160\text{-}180\mu$ longo, $20\text{-}30\mu$ lato, cylindraceo vel fastigato, ad superficiem pertinente; asci clavati vel fusiformes curvatique, $50\text{-}65\mu \times 11\text{-}13\mu$, octospori; paraphyses deliquescentes; sporidia fusiformia, curvata, circa $40 \times 4\text{-}5\mu$, 3-septata, primo hyalina demum flavescentia.

Hab. in thallo vivo Pelvetiæ canaliculatæ, Orkney and Clare Island.

Sections of Pharcidia-infected thalli of Pelvetia, collected in the early part of last autumn, frequently showed spherical or more irregullar masses of very fine mycelium deeply buried in the medullary tissue. These were usually about 200µ from the surface, and in many cases possessed imperfectly developed ostioles. The slender, hyaline hyphæ and soft, white, immersed fruiting bodies were so different from the dark coloured, stouter mycelium and minute, leathery, superficial perithecia of Pharcidia that the two were obviously distinct. However, the absence of any form of spore made it impossible to name or place the fungus at that time. A subsequent examination of Ascophyllum nodosum revealed a fully matured species of similar habit and development for which the the genus Orcadia had to be created. Although this similarity gave a hint as to the probable position of the unknown form on Pelvetia, it was only later, when the mature ascigerous stage was found that it was proved conclusively to be another species of the new genus. The material was collected towards the end of autumn, primarily on account of its showing the late fruiting perithecia of Didymosphæria, but it enabled Orcadia to be identified and its action on the host to be more or less isolated.

The localised mycelium occurs invariably interwoven with the very similar vegetative body of Mycosphærella, in addition it may be with the diffuse Didymosphæria or the rapidly spreading Pharcidia. When their finer branches are so alike, as is the case in the first three, it is almost impossible to make out the relation of any one to the host, or to differentiate their individual action on its cells.

This conjoint occurrence has so far prevented the exact determination of the damage caused to the thallus by *Orcadia pelvetiana*, although a slight local browning of infected regions (Fig. 1, 1) would point to its being a distinct parasite like the other species on *Ascophyllum*.

The fruiting bodies commence to form towards the end of August or in September, but so far no mature perithecia have been observed before October. These are deeply immersed, spherical, possessing, when completely formed, ostioles 150μ to almost 200μ long which pierce but rarely project beyond the decomposed layer overlying the tissues (Fig. 1, 2b). These may be straight or curved,

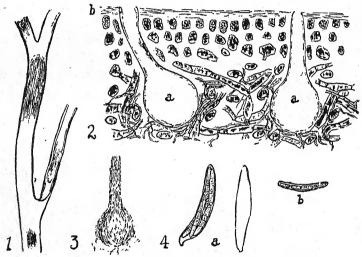


Fig. 1. Orcadia pelvetiana. 1, thallus showing infected areas; 2, section of thallus showing immersed perithecia (a) with long ostioles merely reaching the surface coated with disorganised tissue (b); 3, view of perithecium with woven type of peridium; 4, asci (a), ascospore (b).

ending frequently in slightly dilated tips. The peridium, composed of loosely woven hyphæ (Fig. 1, 3) remains soft and white even where it reaches the surface. This has been observed so far only in the two genera Trailia and Orcadia; all the other marine Pyrenomycetes show a distinct blackening of exposed or unexposed ostioles even when the basal portions remain sub-membranous and slightly coloured, or almost hyaline as in Stigmatea. In the lower part of the perithecium the wall is lined by a layer, 15 to 20μ thick of fine mycelium, forming a substantial cushion from which the asci spring. While the periphyses are numerous as in Orcadia Ascophylli the paraphyses are few and soon disappear.

The presence of asci at all stages of growth points to a successive development of these bodies as in Mycosphærella. They are clavate or fusiform and curved (Fig. 1, 4) with thin tenacious walls within which the ascospores are arranged usually in two sets of four, dovetailed together. The latter are also fusiform, curved, thick-walled, and 3-septate, with the terminal cells longer than the middle two. All become slightly coloured at maturity.

This species is very similar to that occurring on Ascophyllum nodosum. However, there is no doubt of its being a separate species. Not only does it differ from the latter in possessing distinctly smaller perithecia, asci and ascospores; its mycelium spreads less extensively, does little damage to its host and bears perithecia more deeply immersed. This is also borne out by its distribution. Although the two belts of Ascophyllum and of Pelvetia frequently stretch along the beach for a considerable distance in close, almost parallel lines, and the thalli of the former become covered with the black patches indicating attack by its particular species of Orcadia; so far, not only has no corresponding infection of the latter been observed, but the thalli on which Orcadia pelvetiana was found, were collected on rocks near which no Ascophyllum grew.

The reasons for the formation of the genus Orcadia have been already discussed.

DIDYMOSPHÆRIA PELVETIANA NOV. SP. (Fig. 2, 1-4).

Mycelium diffusum, perithecia simplicia, sparsa, minuta, circa 90-115 μ diam., globosa, membranacea, immersa tota, ostiolo brevissimo pseudo-clypeum perfringente: asci crebri, cylindracei vel apicibus attenuatis, 55-75 μ × 9-11 μ , parietibus tenuibus, octospori; paraphyses filiformes vel raro in duos tresve ramos, divisæ; sporidia disticha, fusiformia, 18-24 μ × 5-6 μ , 1-septata, primo hyalina, demum flavescentia, leviter constricta.

Hab. In thallo vivo Pelvetiæ canaliculatæ, Orkney and Solent.

Didymosphæria was found first on attached thalli in the Orkneys and later on sea-borne material in the Solent, thus indicating the probability of a fairly wide distribution, although the writer has failed to obtain it on fixed plants on the South Coast. The limited examination, possible so far, does not, however, preclude the possibility of its occurrence there.

The scattered habit of the perithecia (Fig. 2, 1) hidden all but the ostioles by black coverings, very conspicuous on moist thalli but naturally difficult to detect on dried material, renders it an easy matter to distinguish this species from any of the other fungi occurring on this host. The dark pseudo-clypei stand out very clearly against the olive-green of living or formalin-preserved specimens.

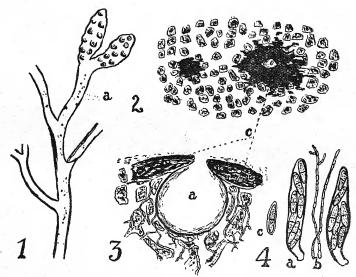


Fig. 2. Didymospharia pelvetiana. 1, thallus of Pelvetia showing the distribution of perithecia (a); 2, surface view with pseudo-clypeus (c) and ostiole (o); 3, section showing perithecium (a), pseudo-clypeus (c); 4, asci (a), paraphyses (b), and ascospore (c).

The mycelium, intermingled with that of Mycosphærella, from which it differs in thickness and parasitic habit, causes little damage to the tissue at first, doubtless on account of its diffused character. In this respect it presents a striking contrast to Stigmatea whose localised mycelium effects the destruction of infected regions in a very short time. Later, browning occurs accompanied by the disintegration of the outer cell layers. How far this is due to the action of Didymosphæria alone it is difficult to decide, as the tissue of the host showed filaments of Elachista clandestina, present often in such abundance as inevitably to cause considerable dislocation of nutrition, if not actual damage. Although the parasitic hyphæ frequently encircle the branches of the latter, no direct connection has been noted between the two. This, added to the fact that the occurrence of Elachista appears to be general on Pelvetia, as

shown by its presence on much of the material cut, points to the association of the two endophytes as being nothing more than coincidence. Some sections showed the thallus so riddled with these two in addition to Mycosphærella that the continued existence of the attacked plant seemed nothing short of the marvellous.

The perithecia are scattered irregularly over the vegetative body of the host. While none have been observed so far, on the receptacles, it is interesting to note that the number of perithecia of the accompanying symbiotic fungus occurring on these is considerably less, owing, it may be, to the presence of the diffused parasite Didymosphæria inhibiting its fruiting. This point, however, requires further investigation. The young perithecium appears in the outer cortex as a mass of thin-walled hyphæ with dense protoplasmic contents, staining deeply; at the same time the superincumbent layers become changed and blackened by the penetration of hyphæ which weave themselves round the cells to form a kind of pseudo-clypeus. This commences to show externally as a slight blackening whose lighter coloured margins extend gradually until a diameter of 175-200 p or even more is attained. Each possesses a fringe of irregular, outward radiating arms as in Fig. 2, 2, and covers a single globose or flask-shaped perithecium whose short ostiole breaks through later. The peridium is nearly colourless in the earlier stages and remains so for some time. Then the ostiole or tip becomes black, and almost carbonaceous, while the outer layer of the basal portion assumes at first a grey and finally a distinct dark colour, retaining, however, its membranous texture. Inside are several layers of fine, soft, closely woven hyphæ, forming a substantial cushion bearing the asci and the simple or occasionally slightly branched paraphyses. The former develop successively, and, when mature, are more or less cylindrical and narrow, or pointed and broad with the ascospores biseriate (Fig. 2, 4 a). The ascospores are elongate, fusiform, uni-septate, with a slight constriction and the ends frequently tapered by the pressure of the narrow containing walls. They become faintly coloured at maturity.

With regard to the relationships of this fungus there seems little doubt. The entire habit and structure shows a clear similarity to several of the species included in Lindau's second sub-division of Didymosphæria corresponding to Microthelia Körb., in which members of that lichen genus have been included, even when the colour of their spores would tend to ally them with Didymella

Sacc. Thus Magnus transferred Microthelia verrucosaria Linds. or Didymella verrucosaria Sacc. to Didymosphæria although it possessed colourless spores. Similarly Zopf placed Didymosphæria pulposi which he found in the apothecia of Collema pulposum, in the same group. The spores of this species are also colourless. D. pelvetiana, just described, occurs under conditions somewhat similar to those experienced by the lichen species mentioned above and presents corresponding structural characters. Its spores, however, become slightly coloured at maturity and thus are more in keeping with the generic character than those of the forms included by Magnus and Zopf.

The present inclusion in this genus of many species provided with a kind of clypeus seems very unsatisfactory especially when it is taken into consideration that this is regarded as sufficiently distinctive a character to separate larger groups as in the case of the Gnomoniaceæ and the Clypeosphæriaceæ. Such anomalies are inevitable so long as any attempt is made to place together in a purely artificial classification forms which, although in their origin and development show natural affinities, differ in the externals on which this classification is unfortunately based.

DIDYMOSPHÆRIA FUCICOLA NOV. SP.

Mycelium diffusum, perithecia simplicia, sparsa, 120- 140μ diam., globosa vel pyriformia, contextu membranaceo, immersa, ostiolo brevissimo atrum pseudo-clypeum perfringente; asci crebri, 70- 90μ \times 10- 14μ , cylindracei vel clavati, octospori; paraphyses filiformes vel apicibus dilatis; sporidia ovoidea, 16- 22μ \times 7- 8μ , 1-septata, primo hyalina demum flavescentia, constricta.

Hab. In thallo vivo Fuci vesiculosi, Orkney.

Until towards the end of last autumn no external sign of fungoid attack had been noted or any species of Fucus, although sections of F. vesiculosus, collected earlier in the season, had demonstrated the presence of hyphæ. Its diffused character doubtless accounted for the absence of any obvious trace of damage until comparatively late.

Only when the perithecia appear is it possible to recognise the infection without sectioning, and even then it is extremely difficult to detect these minute scattered bodies owing to the natural blackening of the thallus of the host.

The mycelium is irregular in thickness, varying from $1.5-2\mu$, and presenting frequently a very much bent and rugged or annulated appearance. It also tends to become slightly coloured. Penetrat-

ing between the cell walls, it finds an easy passage towards the central tissues, through the radial linear series of cells forming the cortex. So far, no haustoria have been observed, although the broken-down appearance of encircled cells would indicate the presence of some form of absorptive organ.

The young perithecia and accompanying pseudo-clypei arise very much as has been described already for Didymosphæria pelvetiana. The masses of fine thin-walled hyphæ, at first irregular in outline and without any distinct limiting layer, force the subepidermal cells of the host apart, breaking down those in their immediate neighbourhood. Gradually the peridia become differentiated. and the ostioles, already blackened, break an opening through the pseudo-clypei, but without projecting. This is followed by a slow darkening of the outer membranous layer of the walls inside which soft hyaline hyphæ form a lining from 15-20μ thick. These globose or flask-shaped perithecia are slightly larger than in the species on Pelvetia and are confined mainly to the persistent thickened midrib portions or so-called stalks of older specimens. They contain bunched together on the basal cushions a large number of cylindrical or clavate asci interspersed with numerous filamentous paraphyses. The former are thick-walled at first, but, after the differentiation of their contents into spores, their walls become thin, though remaining tenacious. The ascospores are ovoid. Their broad upper and narrow, tapering lower ends, separated by a distinct constriction, distinguish them from the usually longer fusiform spores of D. Like the latter they become slightly coloured at pelvetiana. maturity.

The perithecia appear late in autumn and rarely reach full maturity before October.

Smaller fruiting bodies were observed in many of the sections. These differed in shape from the perithecia just described and lacked their characteristic coverings. In habit and structure they resembled the pycnidia of *Stigmatea* but, as no pycnidiospores were found, it is impossible to state definitely whether they are pycnidia or merely imperfectly developed perithecia.

It is interesting to note the frequent occurrence of a species of *Elachista* along with the fungus just as in *Pelvetia*, but here again no connection has been established between the two.

Although this species presents a striking resemblance to D. pelvetiana, the differences in the size of the perithecia and the asci, and in the shape of the ascospores justify their separation.

HYPODERMA LAMINARIÆ NOV. SP. (Fig. 3, 1-5).1

Perithecia in areis rotundis gregaria, immersa, longo elliptica, apicibus aliquid præacutis, 150-200 μ longa, circa 130 μ lata, scissuris longis aperientia, parte superiori atra, carbonacea, basi submembranacea, pallide brunnea; asci clavati apice attenuato, 69-90 μ × 12·5-14 μ octospori; paraphyses filiformes, extremibus leviter inflexis vel dilatis; sporidia disticha, fusiformia vel ovoidea 20-25 μ × 5-7·5 μ primo hyalina, demum parum flavescentia, 1-septata, leviter constricta.

Hab. In thallo vivo Laminariæ saccharinæ, Orkney.

This fungus is a decided parasite found extensively along the shores of the Orkneys, attacking the stipes of Laminaria saccharina and frequently doing considerable damage to them. As their zone is not exposed by the average tide, the ravages of the parasite can be seen only either from a boat, or on the rare occasions, when exceptionally low tides permit the investigator to walk almost dry shod through the Laminaria jungle. Along the narrow and often shelving "sounds" between the islands an easterly wind acting in conjunction with a spring tide lays bare long stretches teeming with rarely uncovered animal and plant life. For several years the writer has had many opportunities of examining thousands of plants in situ and of collecting abundant material. However, as they are broken loose and cast up by every storm, it is always possible to find infected specimens caught in rock pool or strewn along the beach.

The first appearance of attack is marked by a slight local browning which extends its margin rapidly, forming circular or irregular, oblong patches, as in Fig. 3, 1. The brown gives place to black and later the margins merge into one another, so that entire portions of the stalks become discoloured. These are so conspicuous on fresh, moist thalli that they can hardly escape notice.

Sectioning reveals the presence of a strongly developed, irregular dark-coloured mycelium radiating outward from the points of attack. Some of the younger branches are quite hyaline, but the characteristic brown is soon assumed. The cells vary in thickness from 3-12 μ . While some hyphæ extend laterally, others are sent

A very brief preliminary note, embracing the diagnostic and more obvious characters of this species was appended to a recent account of the new genera Trailia and Orcadia (Trans. Brit. Myc. Soc., Vol. 5, 1914); the fuller description of development and structure were reserved until further observations were completed.

down into the cortex but fail to penetrate to any great depth. They all force their passage between the mucilaginous walls very much after the manner of a wedge. This forces the cells apart and they become crushed together into small groups as in Fig. 3, 4. Smaller branches then penetrate between these so that most of the cells become encircled by hyphæ which appear to crush or strangle them and exhaust their contents by means of special bulging haustoria. Frequently the penetrating strands are several cells thick. The attack is confined mainly to the outer cortex, which becomes entirely disorganised ultimately, and, after the maturing of the fungus, breaks down leaving the underlying tissue freely exposed to the many saprophytes of the beach.

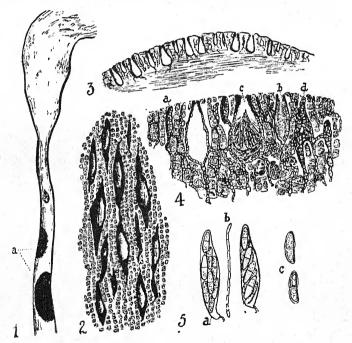


Fig. 3. Hypoderma Laminariæ. 1, stalk showing infected areas (a); 2, surface view of a enlarged; 3, section of thallus with densely crowded perithecia; 4, section of thallus enlarged showing developing perithecium (a), intermediate stage (b), mature form (c) and branching perithecium (d); 5, asci (a), paraphyses (b), ascospores (c).

The perithecia are formed soon after infection, and rapidly develop over the entire blackened area. They are densely crowded together (Fig. 3, 3), and on surface view present the characteristic ostioles of the Hysteriineæ, as depicted in Fig. 3, 2. They are parallel to the long axis of the host, and occasionally open by a

fissure, almost equal in length to the dark, irregularly shaped, carbonaceous, surface smear, but more often the slit is shorter. These perithecia arise from hyphal strands, which become thickened, and massed between the cells immediately below the epidermis as in Fig. 3, 4 a. They are usually dark coloured from the first, but numerous, fine, hyaline filaments are produced inside, and the mass swells quickly. Its longitudinal growth is the more rapid, probably owing to the wedge-like extension of the ends. Along the epidermis a dark stroma-like streak is produced, marking the line of subsequent rupture. In the early stages short filaments grow inwards and cause the perithecia to look very much like pycnidia (Fig. 3, 4, b). The conidiophore-like ingrowths with the hollow, central cavity closely resemble such a structure. But in no case, in the numerous sections examined, have pycnidiospores been observed. Later the entire cavity becomes filled with the ingrowing hyphæ, which, in the basal portion, form a compact tissue. The central mass stains more deeply and later in it appear numerous globular or clavate swellings-the young asci. These develop quickly and crush out most of the sterile hyphæ except the basal pad.

The mature perithecia (frequently regarded as apothecia) are usually elongate with pointed ends; occasionally semi-globose forms were noted, but these are the exception. Peculiar branched or clawed forms, connected by woven strands, as in Fig. 3, 4 d, are frequent. Such connections are indicated also in the surface view (Fig. 3, 2). The depth to which they penetrate into the tissue corresponds very nearly to their length. The bases, normally rounded, are in many cases almost flat. The peridia are thick and carbonaceous at the tip, remaining membranous, although darkcoloured below. The asci and the paraphyses are grouped together on the basal cushion as in Fig. 3, 4 c. The former are club-shaped or fusiform and possess thin walls, while the latter are numerous. simple, and filamentous, with the tips usually bent or slightly dilated. The biseriate, fusiform, or ovoid ascospores have rounded or slightly pointed ends and thick, mucilaginous walls. At first they are distinctly hyaline, but usually at maturity a faint yellowing has been noticed. These mature spores are often guttulate as in Fig. 3, 5 c. They are shed from the wide ostioles in great numbers. or may be set free by the rapid disintegration of the entire infected cortex.

This fungus belongs undoubtedly to the Hypodermataceæ, and is interesting inasmuch as it is the first of this group to be recorded

on marine algæ. The only known genus in that sub-division of the Hysteriineæ into which it can be placed is Hypoderma, with whose characters it agrees very closely in all except the faint yellowing observed in some mature ascospores, as opposed to the hyaline or colourless ones of the type. However, when one considers the absence of standard in the use of these terms, as applied in diagnostic descriptions, and also that the spores are hyaline until almost perfectly mature, when the faint yellowing appears, it is obvious that there is not sufficient ground for making a generic separation. In this connection it is to be regretted that the value in classification of slight colour changes has not been thoroughly worked out. Until more is done in this direction the systematist must inevitably be faced with a distinct difficulty. The uncertainty on this point has led to numerous anomalies owing to the latitude which is frequently taken advantage of.

My thanks are due to Professor J. W. H. Trail, F.R.S., and to Mr. A. D. Cotton, F.L.S., for helpful suggestions. To the latter I am also indebted for Mycosphærella material from Clare Island which showed Orcadia pelvetiana in addition.

The continuous supply of material necessary for the completion of these notes has been facilitated by a grant from the Government Grant Committee of the Royal Society, to whom I wish to express my obligations.

University College, Southampton.

June, 1915.

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¹ For other citations see earlier paper in the NEW PHYTOLOGIST (4 in the list here given).

A CONTRIBUTION TO THE CYTOLOGY AND LIFE-HISTORY OF ZYGNEMA ERICETORUM (KÜTZ.) HANSG., WITH SOME REMARKS ON THE "GENUS" ZYGOGONIUM.

By G. S. West, M.A., D.Sc., F.L.S., and Clara B. Starkey, M.Sc.

[WITH FIVE FIGURES IN THE TEXT].

A LTHOUGH Zygnema ericetorum is a common alga with a world-wide distribution, we have known very little concerning its cytological structure and still less about its conjugation.

During the past few years the authors have been investigating the cytology of various specimens from widely different localities, more especially with regard to the exact nature of the chloroplast. It has also been continuously studied in the field for a period of over fourteen months, and various cultural experiments have been conducted in the hope of inducing it to conjugate.

It can be regarded as the most inert of all the species of Zygnema. Considering that it grows equally well on damp ground and in peaty water, a fact which is not true of any other member of the Zygnemaceæ, and appears very rarely, if ever, to conjugate in these habitats, it may be regarded as an alga which responds very little to the external influences which are known to induce many changes in other green algæ.

Fresh material of both the terrestrial and aquatic forms was studied from various localities in the British Islands, and fixed material from other parts of the world was also examined.

I. CYTOLOGICAL STRUCTURE.

The cell-wall. Tests with chlor-zinc-iodine, iodine and 66 per cent. sulphuric acid, and also strong sulphuric acid prove that the wall consists of cellulose. When tested with strong caustic potash the wall swells greatly and may appear slightly lamellate. During this treatment the phycoporphyrin and the oil-drops pass out through the wall, while at the same time the chloroplast and the two pyrenoids become very distinct. Some filaments possess a more or less distinct gelatinous sheath, often wide, and with a somewhat irregular outline. This feature can be made very evident by the use of potassium chromate and lead acetate.

¹ An account of this work was given by one of the authors before Section K at the meeting of the British Association in Birmingham in 1913. Vide Brit. Assoc. Report, 1913, p. 716.

The chloroplast. In the living cell the chloroplast is very indefinite, and it is scarcely possible to make out its limitations except by the use of appropriate fixing and staining reagents. Very frequently, particularly in material collected in the autumn, the chloroplast is more or less completely obscured by oil-globules. The characters of the chloroplast were most clearly brought out by fixing with corrosive sublimate, then washing in water for twenty-four hours and staining. The most successful stains were Delafield's hæmatoxylin and fuchsin-iodine-green. The latter was used at a strength of 1 vol. of a concentrated aqueous solution of fuchsin to 12 vols. of a 1 per cent. iodine-green solution. The filaments were allowed to stay in this mixture for twenty minutes, then washed in water for a few minutes, taken up through various strengths of alcohol to 95 per cent. alcohol, then transferred to a mixture composed of 100 c.c. of 96 per cent. alcohol, 1 c.c. of glacial acetic

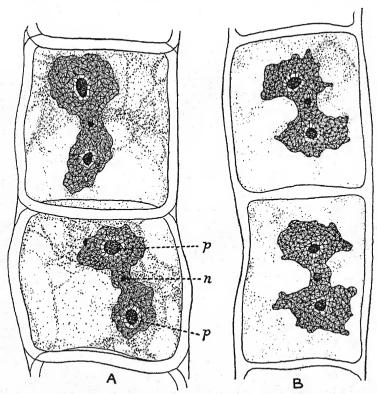


Fig. 1. Two examples of the aquatic form of Zygnema ericetorum from N. Wales. Fixed with corrosive sublimate and stained with fuchsin-iodine-green. \times 1750.

acid, and 0·1 gm. of iodine. In this solution the stain became fixed and the filaments were then transferred to absolute alcohol; finally they were passed into xylol and mounted in Canada balsam. During the process the oil-globules were dissolved out and the cytological details could be clearly seen. The cell-wall was stained a pale blue-green, the general cytoplasm and the chloroplast red, the pyreno-crystal deep red and the starch envelope of each pyrenoid pink. A deeper stained network could be very clearly seen in the chloroplast. The chromatin granules in the nucleus were stained deep blue-green.

With Delafield's hæmatoxylin, and with iron-alum and Heidenhain's hæmatoxylin, the network of the chloroplast, the pyrenoids and the nucleus were all brought out distinctly.

In the diagnosis of the genus Zygogonium given by Wille in 1897¹ he states that the cells possess two axile irregular chloroplasts each with one pyrenoid. In his revision of the Conjugatæ in 1909² this statement is changed to one axile chloroplast with one pyrenoid. Bohlin³ has also made some comments upon the chromatophore of Zygogonium ericetorum. In specimens collected in the Azores, he found that the general cell-contents had much in common with the normal condition found in Mougeotia, and that each cell possessed a band-like chloroplast with two pyrenoids.

The principal alga which of late years has found a place in the supposed genus Zygogonium is Z. ericetorum Kütz., an alga which is widely distributed almost all over the world. An examination of British material of this species, from various localities, and also sundry foreign examples, shows that the previous accounts of the cytology of this alga are far from accurate.

The chloroplast is large and axile, with a variable and most irregular outline. It is often constricted in the middle, sometimes very deeply, and in some cases it is twisted at the constriction. It contains two large pyrenoids, one in each half (consult Figs. 1 and 2). Sometimes in the actively growing filaments the chloroplast is completely constricted, so that there are two chloroplasts in each cell. Very occasionally, in cultures, chloroplasts have been seen with only one pyrenoid, or even destitute of pyrenoids, and on very

¹ N. Wille in Engler and Prantl, Naturliche Pflanzenfamilien, I Teil, II Abteilung, 1897, p. 20.

² N. Wille in Engler and Prantl, Natur. Pflanzenfam., Nachträge zu I Teil, Abteilung 2, 1909.

⁸ K. Bohlin, Étude sur la Flore algologique d'eau douce des Açores. Bih. till K. Sv. Vet.-Akad. Handl. Bd. 27, Afd. III, No. 4, 1901, p. 51, t. 1, f. 3.

rare occasions three or four pyrenoids have been seen in one chloroplast. These conditions, however, are only irregularities since the chloroplast normally contains two pyrenoids.

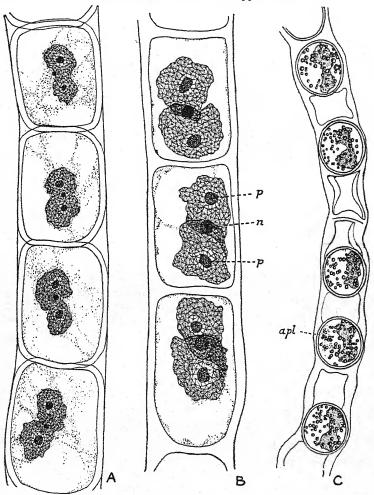


Fig. 2. Zygnema evicetorum. A, aquatic form; B. terrestrial form. Both examples fixed and stained as mentioned in text. C, filament of terrestrial form producing aplanospores on dying. A and B, × 1627; C, × 813.

The nucleus is situated in the central region of the cell, being lodged in the constriction of the chloroplast. It varies somewhat in size, but is mostly very small (cf. Fig. 1 A n).

Reserve material. In the living alga collected in October and in all the examples collected through the winter, the chloroplast is to a large extent masked by numerous oil-globules. These globules

were coloured a deep brownish-red by alcannin solution, were blackened by osmic acid, and entirely removed by ether and absolute alcohol. The oil-globules begin to disappear normally in the late spring. Their presence renders the pyrenoids difficult of detection in unstained examples.

II. EXPERIMENTAL WORK.

This work was primarily conducted in the hope of inducing the alga to conjugate and thus obtaining a possible clue to the physiological conditions essential for its conjugation. All the experiments were failures from this point of view, no conjugation having been observed in a single instance.

1. The Influence of Temperature.

These observations were carried out in one of the natural habitats of the alga in Sutton Park, Warwickshire, from October, 1910 to April, 1911. The place selected was where the alga was growing on damp ground and fortnightly observations were made.

In October, during comparatively mild weather, the filaments were of great length and the chloroplast was completely masked by large oil-globules. At this period the cell-wall had attained a considerable thickness. By the middle of November, colder weather having set in, some of the cells died, causing the filament to become segmented into short lengths of from 2 to 30 cells. The terminal cells of each length were rounded, but did not completely separate, being held together by the walls of the dead cells. At this period the oil-globules were much reduced in size. In January, in which month the ground became frozen, many more of the cells died, the filaments becoming segmented into shorter lengths of cells. the cells contained numerous oil-globules. In February still more cells succumbed and the segmentation of the filament became more marked, each segment consisting generally of about four cells, occasionally of 10 or 20, and sometimes of two or only one. In many cases the filaments became dissociated into the separate short segments, which are of the nature of resting "cysts," 2 consisting

¹ On one occasion, in a culture of the terrestrial form in rain-water. conjugation-tubes were put out from two cells in filaments lying side by side, The ends of these tubes had already started to fuse when conjugation was interrupted by the death of both protoplasts. This was the only instance observed of even an attempt at conjugation.

In the course of the experimental work filaments from different parts of the British Islands were frequently mixed and allowed to grow side by side, but no conjugation took place.

² For previous mention of these "cysts" in the Zygnemaceæ and other Green Algæ consult G. S. West, Treatise on British Freshwater Algæ, 1904; and in Journ. Linn. Soc. Bot., XXXIX, 1909, p. 34.

of only a few cells with thick walls. The "cysts" remained in a state of inactivity until about the middle of March, when the cells showed signs of activity. A new thin cell-wall was formed within the old one, and the resumed growth caused many of the old cells to be broken through. In April growth and division of the cells had produced long filaments. The oil-globules were much reduced, so that the chloroplast and the two pyrenoids could be seen more distinctly.

Similar "cysts" were formed in the aquatic form of the alga, and when examined immediately after the winter condition the resumption of activity was very plainly marked, the old thick walls of the cells being greatly separated by new growth with much thinner walls.

Another terrestrial form from the west of Ireland was cultivated from November, 1911 to June, 1913, the culture thriving on damp peat. By inadvertence it was only examined from January to June, 1913. Numerous aplanospores were formed in January and February, one spore being formed in each cell. A curious fact should be here recorded, viz., that in most cases the whole contents of the cell were not used up in the formation of the spore, a small part of the protoplast being excluded (Fig. 3, D and E). A few cysts were formed, but these were rather unusual. The walls of the spores increased greatly in thickness and the contents turned brown. At the latter end of February the spores germinated and by growth and division filaments of cells were quickly formed.

A quantity of this terrestrial form from the west of Ireland was gradually raised to a temperature of 40°C. It was then allowed to cool slowly, and examined. Many of the cells had been killed; others had suffered no change; but in some the protoplast had rounded itself off and formed an entirely new cell-wall. 50°C. was fatal to all the cells of the filaments.

2. The Influence of Moisture on the Terrestrial Form.

In October, 1910, a number of filaments of the terrestrial form collected in Sutton Park, Warwickshire, were placed in a culture-vessel of rain-water. By November the cell-walls had increased in thickness and the filaments had become segmented into lengths of from 2 to 20 cells. Many of these short filaments of cells became rounded at the extremities and set free. In February, 1911, many cells in each filament were dead and the segments consisted of from

a

 $^{^{\}rm I}$ This is a frequent condition in both terrestrial and aquatic species of ${\it Ulothrix}$ during February and March.

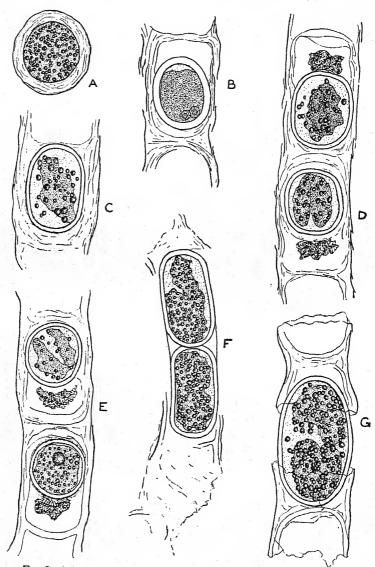


Fig. 3. Aplanospores of Zygnema ericetorum formed naturally. A, represents an escaped aplanospore; the remainder have not yet escaped from the old walls of the mother-cells. All \times 1000.

1 to 10 cells. The cells were loaded with oil-drops. At the end of March most of the cells of each filament were dead and the segments consisted of from 1 to 2 cells only. These were in a healthy condition, containing two pyrenoids in the chloroplast and numerous oil-drops. In April, 1911, the living cells began to grow and divide,

forming new filaments. The material was still alive and in a fairly healthy condition in June, 1912. At this time a few of the cells had become greatly swollen and a new wall, quite spherical in shape, was formed within the old cell-wall. This was a case of aplanospore-formation, and the wall of the mother-cell broke across in order to allow the aplanospores to escape.

Further experiments were made in allowing the alga to dry up. In October, 1910, some of the alga, along with the peaty soil on which it was growing, was put into a damp chamber. It grew very well vegetatively all through the winter. Some of the material was then allowed gradually to dry up from January to March. At the beginning of March the filaments were dismembered into short lengths of from 2 to 6 (occasionally 10 to 20) cells and the cell-walls had increased greatly in thickness. The majority of the dismembered portions consisted of very few cells and were of the nature of thickwalled "cysts." Each cell contained a small chloroplast from which the pyrenoids had disappeared, and oil-globules were either absent or of very small size. It was found that the more complete the drying the fewer the number of cells in the "cysts." When these cysts were subsequently supplied with moisture the cells soon began active division and long filaments were gradually formed.

Some material of the terrestrial form from the west of Ireland was allowed to dry very gradually on its original substratum. This was from March to July, 1913. Many cells died, but both cysts and aplanospores were formed in abundance.¹

3. The Effect of Nutrient Media.

a. Filaments of the aquatic form were placed in a 0.2 per cent. Knop's solution in October. In November the chloroplasts were of a deeper green colour and the cells were dividing rapidly. At the end of February the filaments were of great length and were of a deep green colour. The chloroplasts contained two large pyrenoids, but were mostly hidden by numerous oil-drops which filled almost the entire cell. At the end of March the filaments were very long, quite healthy, and the cells were actively dividing. Some of the chloroplasts possessed three or even four pyrenoids. Occasionally one cell in each filament died, and at that point the filament became disjointed into two pieces.

¹ As an instance of the tenacity of life of this alga it may be here mentioned that the dried material was placed in the dark from the end of July until the end of November. When examined on November 29th there were plenty of short cysts and free aplanospores. In the former the chloroplasts of the cells were quite normal, containing pyrenoids and also, in many cases, oil-globules.

- b. Filaments of the terrestrial form placed in 0·1 per cent. Knop's solution ultimately showed a fragmentation of the filaments similar to that which occurs when the filaments are placed in water, but the fragmentation was delayed much longer.
- c. Filaments of the terrestrial form lived in a very healthy condition in a 0.2 per cent. glucose solution, notwithstanding the fact that there was a considerable growth of fungi in the medium. On the subsequent transference of these filaments to water there was at first no change, but after an interval of two months many of the filaments had fragmented.
- d. Aplanospores were produced on one occasion in filaments of the terrestrial form which had been placed in the dark for a few days after having been grown on agar containing 0·15 per cent. Knop's solution.

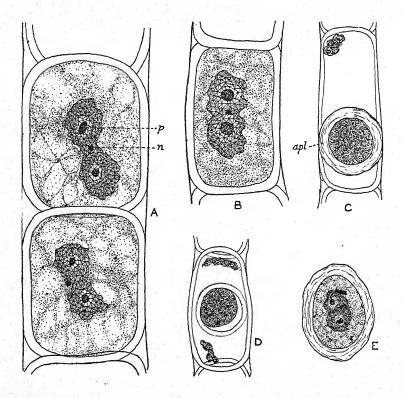


Fig. 4. Zygnema ericetorum from a warm stream in Dominica, W. Indies (described in 1894 under the name of Z pachydermum). A and B, fixed and stained examples to show nature of chloroplast; C-E, aplanospores. apl. aplanospore; n, nucleus; p, pyrenoid. A and B, \times 1477, C-E, \times 738.

III. CAN THE GENUS "ZYGOGONIUM" BE UPHELD?

The genus Zygogonium was founded by Kützing in 1843¹ to include those species of Zygnema Agardh 1824 in which the zygospore was located in the conjugation-tube between the two gametangia. That this distinction is of no value has been shown repeatedly in recent years, since there are species of Zygnema in which the zygospore may occupy any position from the middle of the conjugation-canal to the middle of the female gametangium, all these differences in position being sometimes found in the same pair of conjugating filaments.² Therefore, "Zygogonium" as founded by Kützing cannot be upheld.

In 1858, De Bary³ attempted to establish the genus Zygogonium on an entirely different basis. He described and gave two figures of the conjugation of Zygogonium didymum Rabenh. (=Z. ericetorum type).⁴ From these examples he put forward the view that the conjugating cells first formed "progametargia," which afterwards fused to form a zygospore. Wille in 1909⁵ upheld De Bary's view, although, as previously stated in this paper, his description of the chromatophore was erroneous.

Since the publication of De Bary's figures, the conjugation of Zygnema ericetorum has only once been recorded and that under another name. Figures of conjugating specimens were published by W. and G. S. West in 18946 under the name of Zygnema pachydermnm. The conjugated material was collected by Mr. W. R. Elliot from the surface of mud in a warm stream in the crater of Grande Soufrière in the West Indian island of Dominica. The present authors have re-examined the original material of Z. pachydermum and find that it cannot in any way be specifically separated from Z. ericetorum. The structure of the chloroplast is exactly the same

¹ Kützing, F. T. Phycologia generalis, Leipzig, 1843.

² West G. S. The Algæ of the Yan Yean Reservoir. Journ. Linn. Soc. Bot. XXXIX, 1909; Transeau, E. N. New species of Green Algæ. Amer. Journ. Bot. I, 1914, p. 289.

² A de. Bary, "Untersuchungen über die Familie der Conjugaten." Leipzig, 1858.

⁴ Through the kindness of Dr. A. B. Rendle one of the authors has most carefully examined the original specimens of Zygogonium didynum Rabenh. Alg. exsic. No. 182. (=Z. Agardhii Rabenh. Flor. Europ. Alg., III, 1868, p. 253) in the Herbarium of the British Museum. These specimens are identical in all respects with typical Zygnema ericetorum.

⁵ N. Wille in Engler and Prantl, Natur. Pflanzenfam. Nachträge zu I Teil, Abteilung 2, 1909.

W. and G. S. West in Journ. Linn. Soc., Bot., XXX, 1894.

(compare Fig. 1, A and B with Fig. 4, A and B) and the thickness of the cell-wall is no greater than is often the case in the terrestrial form of Z. ericetorum. The aplanospores of this West Indian form were also similar to those of the terrestrial forms of Z. ericetorum (compare Fig. 3, A-C with Fig. 4, C-E). The great interest lies in the conjugating examples. The conjugation was exactly as in those species of Zygnema in which the zygote is lodged in the conjugation-canal (vide Fig. 5) and in no instance was the formation of "progametangia" observed. De Bary's figures of conjugating Zygogonium

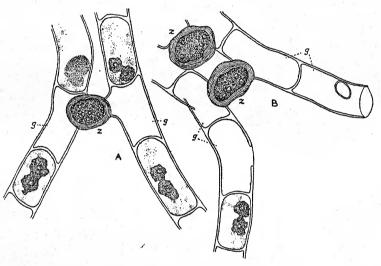


Fig. 5. Two conjugated examples of Zygnema ericetorum from a warm stream in Dominica, W. Indies. \times 384. g, empty gametangia; z, zygospore.

didymum do not give one the impression of healthy conjugation, but rather appear to be abnormalities. It would seem, therefore, that the genus "Zygogonium" of De Bary is founded upon two abnormal examples of conjugation, in consequence of which it cannot be upheld. Moreover, even if De Bary's contentions were verified and it became necessary on account of the conjugation of this alga to place it in a genus apart from Zygnema, the name "Zygogonium" could not be used since it would be altogether at variance with Kützing's use of it in 1843 and in subsequent works.

The only characters which separate Zygnema ericetorum from the other species of Zygnema are those of the chloroplast, but they are not of sufficient importance to warrant the creation of another genus for its reception.

SUMMARY.

In each cell of Zygnema ericetorum there is normally only one large axile chloroplast of indefinite outline. It is usually constricted in the middle and in some cases twisted. There are two large pyrenoids, one in each half of the chloroplast. In very many cases the chloroplast is partially or wholly masked by numerous oilglobules.

There is experimental evidence that a low temperature causes a thickening of the cell-wall and the production of cysts.

Filaments of the aquatic form grow well in a 0.2 per cent. Knop's solution.

Filaments of the terrestrial form when placed in water gradually fragment and become dissociated into short lengths of cells; which may, however, ultimately grow into long filaments. If placed in 0·1 per cent. Knop's solution similar fragmentation occurs, but is longer delayed.

When allowed to dry gradually, the filaments fragment into thick-walled "cysts."

The genus Zygogonium as founded by Kützing (1843) is untenable, and available evidence does not support the retention of Zygogonium on the basis put forward by De Bary (1858) and Wille (1909).

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A JURASSIC WOOD FROM SCOTLAND.

By RUTH HOLDEN.

[WITH PLATE III].

THE Jurassic strata of north-east Scotland have been known in a general way since the time of Hugh Miller (11), but it is only comparatively recently that they have been accurately correlated with those of England and of continental Europe. A concise account of their lithological and palæontological character is given by Mr. H. B. Woodward (14), while the plant remains are described in detail by Seward (14), Seward and Bancroft (15), and Stopes (17). Up to the present, there has been but one structurally preserved specimen of petrified wood found in that region, viz., Cedroxylon Hornei from the Upper Oolite of Helmsdale (15). Dr. E. A. Newell Arber, however, secured a large specimen from the Corallian of

Loth, which, when sectioned, proved to be admirably preserved, and this he kindly submitted to the writer for investigation. It is about 12 inches long, and roughly oval in cross section, 15 inches being the long diameter and 6 inches the short. It is covered externally by a thin coating of lime, and there are calcite veins shooting in every direction; it is, in fact, very similar to those specimens which are strewn so abundantly along the shore, six miles further north, at Helmsdale.

The annual rings indicate that this stem had attained an age of at least 75 years, but it is quite possible that originally there were more layers which have now been stripped off. Although their contour shows that the centre is present, the tissues of that region have become displaced, and it is now impossible to decipher the structure of the pith or of the primary elements.

The character of the secondary wood is represented by the photographs of Plate III. The annual rings are well marked, and vary in breadth from 2 to 11 mm. The spring wood grades evenly into that formed in summer, indicating that we are dealing with a stem, not a root. In longitudinal section, the wood is seen to be very simple, consisting only of tracheides and rays, without resin canals or wood parenchyma. The rays (Pl. III, Fig. 2) vary from 2 to 20 cells in height, averaging 8 to 12; in general they are uniseriate or partially biseriate. The pitting is seen in radial longitudinal section to be of the Abietineous type-cf. Gothan (5). The transverse walls are thick and heavily pitted, as in the living Abies or Picea; the pits of the tangential walls are not so numerous as in those genera, but resemble more closely certain of the Cupressineæ, e.g. Juniperus. Radially there are one, or less frequently two, half-bordered pits to each cross-field, similar to those of Podocarpus, or certain species of Pinus. The pits of the tracheides are confined to the radial wall, where they are strictly uniscriate, and almost invariably closely compressed and flattened by mutual contact (Fig. 4). The pore itself was originally circular, but during the course of petrifaction the wall of the tracheide has usually become slit obliquely, along the pit, thus obscuring the true condition. Such an appearance may be often observed in dried specimens of living conifers, especially in the thick-walled summer tracheides. It is usually unsafe to make a definite statement regarding the torus of a fossil, but in this case, there can be no doubt of its presence. It is dark in colour, and circular in outline, and contained within the opening of the pit. As is well known, in the Abietineæ the torus is considerably larger than the pore; in the

Podocarpineæ, the reverse is true—the torus is much reduced (or rudimentary?) and distinctly smaller than the pore; while in the normal wood of the living Araucarineæ, as in the Cordaitales, Cycadales and ancient gymnosperms generally, it is lacking altogether. In a number of fossil Araucarians, however, it has been described—e.g. Paracedroxylon (16) where it is of the same type as in this specimen in question. Another feature which in this specimen resembles the conifers and Gentales (18) is the presence of trabeculæ. These should be distinguished from "bars of Sanio," or "rims," as Groom (7) prefers to call them. By the former are meant lignified bars which cross the lumen of a cell: by the latter, cellulose thickenings embedded in the substance of the wall itself, between the bordered pits. Trabeculæ occur indiscriminately throughout the coniferous series; rims of Sanio are present in the Abietineæ, Cupressineæ, Podocarpineæ and Taxineæ, but never in the Araucarineæ, living or fossil. They are quite unrepresented in this specimen. In addition to the trabeculæ. there are other cross partitions, occurring very abundantly and easily recognized by their thinner, more delicate walls, and generally curved contour. Figs. 2, 3 and 4 show how extremely numerous they are. These are unquestionably tyloses, for in tangential section it is possible to obtain stages of their outgrowth from the cells of the medullary rays. Preparations were made from all parts of the stem-near the pith and at least in the 50th year, and from each end-but the tyloses were uniformily present. The subject of tyloses in the tracheides of conifers has long been a disputed point. Molisch (12) stating that they are altogether lacking, while Raatz (13) considers that wounds induce their formation in various species of Pinus, Picea, Larix, Thuya, etc. In 1908 Chrysler (3) re-investigated the whole question and, after a comprehensive examination of numerous representative genera, concluded that Pinus is the only genus where tyloses occur, and then only in the heart wood of the root and the cone axis. Wounds, in general, bring about a better development in these restricted regions, but do not cause them to appear in other regions or other genera. This condition is strikingly different from that recorded by Brooks and Sharples (2), where the traumatic stimulus given, in this case by a fungus, caused the formation of tyloses in the vessels of Heven brasiliensis, whereas in the healthy wood they are completely absent. Bailey (1), however. has seen indications of them in the normal stem wood of several species of Pinus, and Conwentz (4) has described them from Eocene material. In none of these cases are the tyloses so abundant as in the fossil under consideration, where they fill the lumen of almost every tracheide. In addition to tyloses and trabeculæ, there is a third variety of cross partition—the so-called "resin spools." These are very characteristic of the Araucarineæ, both living and fossil; see Thomson (19), Lignier (10) and Jeffrey (9).

We come now to the affinities of this fossil, and the extraordinary development of tyloses recalls immediately Protocedroxylon araucarioides, described by Gothan from the Upper Jurassic of Spitzbergen (4). Not only in this feature is the resemblance close, but also in the combination of Araucarian pitting of the tracheides and Abietineous pitting of the rays. Specimens of the same structure were found by the writer (8) in the Lias of Scarborough (Yorkshire) and described as Metacedroxylon araucarioides, the generic name being changed to avoid an implication of Abjetineous affinities. In two respects, however, this wood differs from the Yorkshire and Spitzbergen specimens—the lack of tangential pitting, and the frequently biseriate character of the rays. Although these may seem relatively unimportant points, recent investigations of living conifers indicate that both are remarkably constant. For example, tangential pits are uniformly absent in hard pines, but are abundant in the summer tracheides of soft pines and of the remaining genera of the Abietineous series, while in the Taxodineæ and Cupressineæ they may occur scattered throughout the year's growth. As regards rays, these are typically uniseriate in the Coniferales as a whole, but in Sequoia sempervirens biseriate ones occur even more frequently than in the case of this fossil. It seems best, accordingly, to institute a new species for this specimen, and to denote its source, it may be called Metacedroxylon scoticum.

SUMMARY.

From the Corallian of Loth, there has been described a coniferous wood, characterised by a combination of Araucarian pitting of the tracheides and Abietineous pitting of the rays, and by a remarkable abundance of tyloses in the tracheides. For this specimen the name of Metacedroxylon scoticum is proposed. It differs from Metacedroxylon araucarioides (Protocedroxylon araucarioides Gothan) only in the absence of pits on the tangential walls of the tracheides, and in the biseriate character of the rays, and it confirms the conclusion of Dr. Stopes that the plants of the Scottish Oolites belong to the same "life province" as that which included Yorkshire—to which we may add Spitzbergen—during that period.

BOTANY SCHOOL, CAMBRIDGE, April, 1915.

DESCRIPTION OF PLATE III.

ILLUSTRATING MISS HOLDEN'S PAPER ON A JURASSIC WOOD FROM SCOTLAND.

Fig. 1. Metacedroxylon scoticum; transverse section, showing character of annual ring.

Fig. 2. Same; tangential section, showing uniseriate and biseriate rays, and abundance of tyloses in the tracheides.

Fig. 3. Same; radial section, showing width of annual ring, and general character of the wood.

Fig. 4. Same; radial section, showing cround uniseriate pits of the tracheides, tyloses and ray pitting.

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CHARLES GLASS PLAYFAIR LAIDLAW.

C. G. P. Laidlaw is the first British botanist, so far as the present writer is aware, to fall in the war.

Laidlaw was born in 1887 in London, but was of pure Scottish descent. He was the son of Dr. Robert Laidlaw who was born in Ayrshire and took his doctor's degree at Edinburgh. Later he engaged in medical missionary work and was afterwards Government Medical Officer for the Seychelles. Dr. Laidlaw married Elizabeth Playfair, daughter of Patrick Playfair of Glasgow and Ardmillan. In 1897 Dr. and Mrs. Laidlaw moved to Cambridge for the sake of their sons' education and Charles went to the Perse School. He was distinctly good both at his work and at games. While still at school he was asked to play for the University water-polo team when they were a man short; and before he left he was head boy on the Science side. Later he played lacrosse for his College and sometimes for the University, though he did not get his half-blue. He was also a sound lawn tennis player.

In 1906 Laidlaw was elected to an Entrance Scholarship for Natural Science at St. John's College and began "residence" in October, 1907, afterwards obtaining a Foundation Scholarship. His Scholarships paid all his University expenses. In 1909 he was placed in the First Class of the Natural Sciences Tripos, Part I, and in 1911 obtained a First Class (in Botany) in Part II of the same Tripos. He was then elected to a Hutchinson Studentship at St. John's College, and undertook research in Plant Physiology at the Botany School under the direction of Mr. F. F. Blackman. He worked at an electrical method of determining carbon dioxide in relation to photosynthesis, and in 1912 was elected to a Frank Smart Studentship at Caius College with a view to his continuing this work, which was progressing most promisingly. At the same time however, he was offered a Research Scholarship by the Board of Agriculture, and as this seemed at the time to lead to a more assured future career, he decided after some hesitation to take up the Government Scholarship, and to abandon the Cambridge one. This decision unfortunately necessitated the abandonment of his work at Cambridge and his migration to London by direction of the Board of Agriculture. From the autumn of 1912 till the outbreak of war in August, 1914, Laidlaw worked under the direction of Professor V. H. Blackman of the Imperial College of Science and Technology. Here he was engaged on an investigation of the

physiological conditions of plants forced under glass: he also worked on the effect of temperature on the rate of growth of a fungus, *Sclerotinia libertiana*. Both these investigations, which presented considerable difficulties, were left incomplete. In collaboration with Mr. R. C. Knight (also a Board of Agriculture scholar) Laidlaw invented a new type of recording porometer for investigating changes in the size of the stomatal pore.

Thoroughness and carefulness were the marks of Laidlaw's research work. With these he combined a sound critical intelligence, and in the opinion of those best qualified to judge, he would, had he lived, certainly have carried his physiological work to a successful conclusion and obtained valuable results. Professor Blackman writes of him: "A somewhat shy manner and a certain cautiousness in committing himself—perhaps related to his Scotch descent—failed to hide a very attractive nature."

In the autumn of 1914 he joined the London Scottish as a private, and after a period of training left England for the front on March 10th. On Good Friday morning, April 2nd, he was in the trenches at Richebourg l'Avouée, resting in the sun behind the barricade in an apparently perfectly safe place. A rifle bullet penetrated a sand-bag at a weak spot and struck him below the shoulder near the third rib, inflicting a wound which his comrades, at the time, thought not dangerous. He received first aid at once, and about mid-day was taken to the dressing station, and later to the 3rd Field Ambulance Hospital at Béthune. There it appeared there was much internal hæmorrhage, and nothing could be done beyond making him as comfortable as possible. Towards midnight he began to sink and died about 1.45 on the morning of April 3rd. He was buried in the cemetery at Béthune.

Everyone who knew Laidlaw was fond of him. He was a man of that absolutely straight pure type of character which is so unmistakable when we meet it. Of singularly gentle disposition and manner, he was always helpful, unselfish and to be depended on. From relatives, from old school and college friends, from his teachers, fellow students and fellow workers, the same story comes. He was a simple, straight, sweet-natured gentleman, and a really devout Christian.

Laidlaw joined the army not because he loved fighting, nor because he was carried away by patriotic passion, but against his inclination and simply from a high sense of duty. It is such as he among the men who fall that we cannot but honour the most.

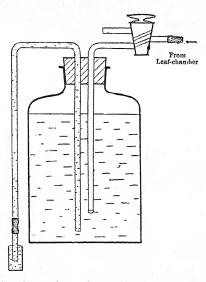
A CONVENIENT MODIFICATION OF THE POROMETER.

By R. C. KNIGHT, B.Sc.

[WITH ONE FIGURE IN THE TEXT].

N the Darwin and Pertz form of the porometer air is drawn through the leaf by means of a column of water, the rate of flow of the air being measured by the rate of fall of this column, and this rate is taken as an indication of the size of the stomatal pores.

A column of mercury in a narrow-bore horizontal tube with a short vertical arm at one end, dipping into a reservoir of mercury, can be used instead of the vertical column of water, thus obviating the change of pressure which occurs as the water falls, but in both these forms the water or mercury needs to be raised to its original position after every reading.



After working for a short time with the above-mentioned types, a device was adopted which proved itself more convenient than either, and which is also free from many of their drawbacks.

The pressure difference required to draw air through the leaf is obtained by means of a head of water in an aspirator bottle, and this pressure difference is kept constant throughout the experiment by the usual expedient of keeping below the surface of the water the opening of the intake tube, with which is connected the chamber

¹ Proc. Roy. Soc., 84. B., 1911, p. 136.

attached to the leaf, so that the air drawn through the leaf bubbles through the water. Any required pressure may be obtained by adjusting the length of the out-flow tube, which dips into a small overflow vessel, or, alternatively, the water may be allowed to drip from the end, though in the latter case there are slight pressure changes due to the formation and discharge of the succession of drops.

It has been found convenient to insert a three-way stopcock between the leaf chamber and the aspirator bottle in order to place the chamber in connexion with the outer air, and so release the pressure upon the leaf, when no reading is being made.

The time elapsing between the discharge of two consecutive bubbles from the air-intake tube is taken as an indication of the size of the stomatal apertures, and this period can be determined with considerable accuracy by means of a stopwatch.

The form of the apparatus is shown in the accompanying diagram.

Compared with the Darwin and Pertz form, this aspirator method shows to advantage, and at the same time presents but few difficulties.

- 1. The pressure drawing the air through is constant, except for very slight variations as each bubble forms, and even when these variations have the greatest effect, i.e., when the pressure difference employed is small, the cycle will be the same for every bubble and therefore will not detract from the accuracy of measurement.
- 2. The need for raising a water or mercury column for each separate reading is eliminated and this is a great convenience when several consecutive readings have to be made.
- 3. With any particular setting of pressure, area of leaf chamber and size of bubble, the method is applicable to a wide range of stomatal changes, since, if the rate of air-flow increases sufficiently to render impossible the accurate timing of one bubble, any number may be included without inconvenience and an average obtained. Using the Darwin and Pertz method, the same contingency may be met either by altering the average pressure, thereby necessitating a calculation, or by maintaining the same average pressure and altering the distance through which the column falls. In either case there is a possibility of introducing an error into the reading. When the pressure inside the leaf chamber is reduced in order to draw air through the leaf, there is a natural

tendency for the pressure difference to cause a curvature of the leaf, so that the portion to which the chamber is attached tends to become convex on the side towards the chamber. In the case of thin leaves especially, this curvature is quite obvious even when a small pressure difference is employed. Obviously there is some likelihood that this change of shape has some mechanical effect upon the size of the stomatal pores. If the pressure difference is nearly constant, as in the aspirator method, this artificial alteration, if any, of the size of the pores is constant throughout, whereas in using the Darwin and Pertz form, if it becomes necessary to alter the pressure relations obtaining in the system, there is a considerable danger of affecting the stomata differently at different times, thereby impairing the accuracy.

4. The quantity of air in the bubble is, of course, an important factor in the aspirator method, since, if the bubbles vary in size irregularly, error is unavoidable.

The pressure difference in the aspirator bottle, being practically constant throughout the experiment, does not enter into consideration, but there are other conditions which are liable to vary as the experiment proceeds, and which may affect the bubble. Change in the rate of the air stream is, of course, of constant occurrence, and experiment has shown that an increase in this rate results in an increase in the volume of the bubbles, which was perhaps to be expected. An increase in the speed of the air stream from 13.7 c.c. per hour to 259.2 c.c. per hour, which is comparable to the range encountered in some plants, resulted in an increase in the size of the bubbles of nearly 4%. This is relatively a very small amount, probably within the limits of the experimental error, and may therefore be neglected.

A second factor which varies as the experiment proceeds, and which might affect the size of the bubbles, is the depth at which the bubbles are discharged. As air is drawn into the aspirator bottle, the water level falls, and the bubbles are discharged nearer and nearer to the surface. Experiment has shown, however, that the variation in size of the bubbles with varying depths is practically negligible—the differences observed being less than 1% for a difference of depth of 7 cms. (10.5 cms. to 3.5 cms.).

A change of temperature, by affecting surface tension, is also liable to bring about change in the dimensions of the bubble. Experiments at different temperatures have been carried out and have shown that considerable variations are possible. An apparatus which at 15.9°C, delivered bubbles of average volume 0.126 c.c.,

at 37.9°C. gave bubbles containing 0.115 c.c., a decrease of nearly 9%. This temperature range is, however, far greater than need be experienced in actual work. If the aspirator is shaded from direct sunlight the temperature change need never be more than 5°C., the effect of which is negligible.

5. Temperature changes are obviously liable to interfere with the system in ways other than that described above. A rise of temperature would cause an expansion of the air already in the aspirator, and although this would be almost immediately compensated by the exit of water, it is conceivable that there might be some slight temporary effect upon the rate of bubbling. Sudden temperature changes should therefore be avoided, such as might arise from filling the aspirator from the tap and immediately beginning an experiment in a warm laboratory. Ordinary temperature changes in a laboratory or greenhouse are so gradual as to be negligible, especially as each reading need occupy only a few seconds. If greater accuracy is required the aspirator may be placed in a water bath.

A description of a typical experiment will perhaps best serve to indicate the details of the apparatus and the method of use.

Exp. 56; December 16th, 1914.

The volume of the aspirator bottle was nearly two litres, the air-intake tube at which the bubbles formed, 4 mms. internal diameter, and the pressure difference 13 cms. of water. The plant used was Eucharis Mastersi, the stomata of which are capable of opening very widely under suitable conditions, and occur only on the under surface of the leaf. The leaf chamber enclosed an area of about 1 sq. cm. and under these conditions, the day being bright with cloudy intervals, and the plant in a greenhouse at about 20°C., at 10.30 a.m. the time taken for one bubble to form and discharge was 2.9 seconds, five bubbles being actually timed and an average obtained from these. By 12.10 p.m. the time for one bubble had decreased to 1.8 seconds (average of 10), whilst the last reading, taken at 4.10 p.m., twenty minutes after sunset, was 21.2 seconds for one bubble, with the stomata closing rapidly.

As deduced from these rates of bubbling, the apertures of the stomata in this experiment, as has been indicated, were rather larger than the average, but higher rates are sometimes found, especially with plants the leaves of which have stomata upon both surfaces. Helianthus tuberosus on October 1st, 1914, a very bright hot day, with apparatus similar to that in the experiment already

quoted, except that the pressure difference was 5 cms. gave a reading at 11.25 a.m. of 0.26 seconds per bubble (30 bubbles timed) and by 4.20 p.m. on the same day, the time for one bubble was more than 300 seconds. This was an extreme case, and in general the conditions of the experiment are arranged so that a bubble never takes less than one second to form, a very rapid stream, besides being difficult to time, being liable to cause one bubble to interfere with the next. At the other extreme, readings of hundreds of seconds can hardly be regarded as anything but an approximate average, for in two or three minutes some stomata may open or close to a considerable extent.

Whenever possible, each reading is taken three times in rapid succession, and the mean is regarded as an indication of the stomatal aperture, unless this is changing very rapidly as is sometimes the case towards evening.

Imperial College of Science and Technology, May, 1915.

PRELIMINARY OBSERVATIONS ON THE POLLINATION MECHANISM OF ARCTOTIS ASPERA LINN.

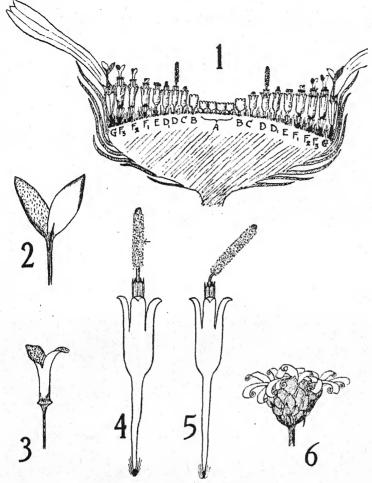
By James Small, B.Sc. (Lond.), Ph. C.,

Demonstrator in Botany, Armstrong College, Newcastle-on-Tyne.

[WITH SIX FIGURES IN THE TEXT].

Learnes of Centaurea cyanus, but it is not so widely known that other cases of irritability occur in the Compositæ, especially in the Cynareæ, e.g., Centaurea montana, Centaurea dealbata, Carduus Kerneri, Silybum marianum, Gerbera multiflora. There are also other examples. In the allied tribe, Arctotideæ, is the species under consideration, but in this case it is the style which is sensitive. The course of events is unusually complex and a description of the composition of the capitulum and of its development from the bud is the clearest method of explaining the behaviour of the florets.

^{&#}x27;Since this paper was written, my attention has been called to the fact that M. von Minden ("Reizbare Griffen von zweier Arctotis-Arten," Flora, Bd. 88, 1901, p. 238) has described in some detail, though without figures, the movements of the style in Arctotis aspera and A. calendulacea. I have been unable to see Minden's paper, but am informed that his observations are precisely similar to those here recorded. However, it has seemed worth while publishing the present account, especially as no figures appear to have been published previously to illustrate the interesting facts observed.



Figs. 1-6. Arctotis aspera.

Fig. 1. A semi-diagrammatic median section through a capitulum. For details see text. Fig. 2. Style of ray floret. Fig. 3. Style of hermaphrodite floret in female stage. Fig. 4. Male floret in irritable phase before being touched. Fig. 5. Male floret after the style has been touched as indicated by the arrow in Fig. 4. Fig. 6. General view of the capitulum showing curling of the ligulate corolla ready for the fruiting stage.

Composition of the Capitulum.

The centre of the disc is occupied by from five to seven rings of male florets, Fig. 1, A-E, tubular and sterile, with a very rudimentary pappus or none at all. The style acts solely as a pollen presenter. Outside these there is a ring of tubular hermaphrodite florets, F1, which vary in different capitula but which are usually much the same as the F2 and F3 florets, the pappus being similar

but smaller. The fertility varies so that in some capitula these florets are sterile and the style acts only as a pollen presenter.

In the outer rings, Fig. 1, F2 and F3, the florets are always hermaphrodite and tubular with the pappus composed of five wide membranous scales. Attached to the base of the florets are a number of setæ similar to those which cover the receptacle. The ray florets are in one row, ligulate with no stamens and with the style of a different type (Fig. 2) from that of the disc florets (Fig. 3). The receptacle is covered with setæ which are more or less membranous.

Pollination Mechanism.

When the young capitulum opens the ray florets spread out disclosing a disc which is nearly flat. The first sign of activity occurs in the F3 row, where the corolla has, during the previous night, elongated but remained closed as in Fig. 1, B. The corolla opens out and the staminal tube is seen to be closed at the top by five nearly black apical appendages. As it is a South African species all the activities of the florets are best seen when the flower is examined on the plant in a greenhouse during warm, sunny weather. Under such conditions the corolla breaks open about 8.30 a.m. in June. Half an hour later a few of the florets show the tips of the styles emerging from the staminal tube and by 10 a.m. most, if not all, the florets in the active row have the style aa shown in Fig. 1, D and Fig. 4. Each style takes from five to ten minutes to emerge under the best conditions, but if the atmosphere is cold or the plant is in deep shade the styles may not come out at all, or they may come out only partially, or they may come out entirely but very slowly. Under good conditions of light and temperature, however, the process of pollen presentation can be seen very clearly within a few minutes.

One of the peculiarities of the style in this stage is that it is sensitive to touch and moves quickly in the direction of the touch. The arrow in Fig. 4 indicates the point of contact and Fig. 5 represents the position assumed as a consequence by the style. This irritability is shown immediately the upper hairy portion of the style is free of the staminal tube. The tip of the style formed by the two closely adpressed branches of the stigma has no pollen upon it but the remainder of the thick part of the style is completely coated with the yellow sticky particles.

When the flower head is in a vigorous condition the style recovers quickly from the movement and regains its irritability in less than half a minute. It remains in the position assumed after the reaction until touched again. It has been observed, however, that when a style has been touched and has reacted in a given direction a longer time elapses before it will react in the opposite direction. Accurate time observations of these reactions would be interesting from a physiological point of view, but have no direct bearing on the present subject.

After the first day of the male stage the style is withdrawn completely within the staminal tube, usually starting about 4 p.m. and retiring slowly. Sometimes very little pollen is scraped off as the style is retracted but more frequently a distinct ring of pollen is left adhering to the top of the staminal tube (Fig. 1, E). In the case of the F3 florets the style emerges the following morning slowly and in the female stage (Fig. 3). Then it is not sensitive to touch and has no pollen attached to the outside which is now comparatively smooth. The F2 and F1 florets act similarly. One or two rows of florets grow up each night in regular succession until the whole of the disc florets have opened. In the female stage, however, the styles of the F2 florets are not exserted to the same extent as those of the F3 florets and those of the F1 are exserted less than those of the F2 florets. The florets lying inside the F1 row exsert irritable styles in the same way as the outer florets, but in these the style may emerge for two or even three successive days in the male stage and is retracted during the intervening nights. Little or no pollen is scraped off the first evening but on the second and third days all the pollen is removed from the style as it withdraws into the staminal tube. The ring of pollen is very distinct during the first twelve or eighteen hours lying around the top of the staminal tube, but gradually breaks up and a powdery mass is left around the top of the floret. The styles in these florets are not exserted again after the male stage is past.

As a rule there is only one row of styles in the irritable phase each day but sometimes two rows mature more or less simultaneously, the inner row emerging later in the morning of the same day or the following morning at the same time as the styles of the outer row are exserted.

The styles of the ray florets become gradually more and more exserted up to the time of fruiting, making their first appearance while the F2 florets are in the male stage. They are not retracted during the night nor are the styles of the F florets in the female stage. When the last disc florets are in the active stage the

corolla of the ray florets begins to curl up like a watch spring and when about half the corolla is twisted all the ray florets bend over and cover the disc, thus initiating the fruiting stage of the capitulum. While the disc florets are active the ray florets close up every night, producing the well-known nocturnal condition of the capitulum but with no curling of the tip of the corolla.

In Arctotis aspera Linn. (syn. A. aureola) we have the following noteworthy points. (1) Three types of florets—female, hermaphrodite and male. (2) Irritable styles in the disc florets. (3) Diurnal exsertion and retraction of the styles of the disc florets. (4) Diurnal progression of maturity towards the centre of the disc. (5) Permanent withdrawal of the style of the inner florets after the work of pollen presentation is completed. (6) Nocturnal closing of the capitulum by the ray florets.

As material and opportunities for constant observation were not available I hope to make more detailed observations when military exigencies permit. In conclusion I would express my thanks to Mr. R. Irwyn Lynch, M.A., for material and for the opportunities given for the study of this interesting member of the Compositæ during the time I was recovering from a shrapnel wound in a Cambridge hospital.

FOREIGN POLLEN IN FOSSIL SEEDS.

By F. W. OLIVER.

THE appearance of Mr. Birbal Sahni's short but interesting paper on Foreign Pollen¹ tempts one to contribute a brief note on the same subject. Mr. Sahni records the fact that of the ovules of Ginkgo investigated, about a dozen in all, no less than eight contained foreign pollen grains. Among these, three distinct species of grains were discriminated, whilst in at least one instance a pollen grain of foreign origin was found to have germinated, producing a tube.

As the author justly remarks, the conditions which prevail in botanic gardens and similar artificial habitats are particularly favourable to occurrences of the kind. Provided the liberation of wind-borne pollen synchronises with the presence of collecting drops at the micropyle there is no obvious reason why the pollen grains should not find their way to the pollen chamber—so long of course as they conform in the matter of size.

¹ New Phyrologist, Vol. XIV, 1915, p. 149.

During the last twelve years hundreds of palæozoic fossil seeds must have passed through my hands and it is surprising to find how rare is the occurrence of mixed pollen in the pollen chamber. What has always impressed me, with cumulative effect, has been the purity of the pollen. So far as my experience goes the case of Stephanospermum akenioides alluded to by Mr. Sahni¹ remains a "solitary instance" of departure from this rule. Not that puzzling objects do not occur in pollen chambers. But in this case alone have I felt that the identification of such objects as "foreign pollen" was reasonably certain.

On more than one occasion I have remarked on the abundance of pollen present in the pollen chambers of fossil seeds. *Physostoma elegans* is pre-eminent in this respect. In my description of this seed an instance of the occurrence of nearly fifty grains was recorded.² I have in my possession two other sections of *Physostoma* worthy of mention. One, a transverse section, shews forty pollen grains; the other, median longitudinal, eighty. What is remarkable is that the pollen does not seem to be contaminated in either case.

Curiosity as to the circumstances which brought so much pure pollen into these pollen chambers has not been gratified. The possibilities may, however, be formulated as follows. In the event of aerial transport either the drop mechanism remained in operation for a prolonged period or else the pollen was discharged into the air at no great distance in dense clouds. Otherwise, some such agency of transport as insects must have come into play.

The latter alternative was in the mind of Sir Joseph Hooker when he wrote "Has anyone accounted for the quantity of pollen grains in the sac of the ovule of Cycadeæ—so many more than the wind is likely to have brought?" s

The suspicion of insect agency has gained a certain amount of indirect support from occasional isolated observations on Cycas, Welwitschia, etc. Without pursuing this particular matter in detail on the present occasion, it is allowable to say that pollen purity is not only perfectly consistent with insect agency but is just what might be expected in view of the habit commonly attributed to e.g. bees, of confining their visits as they go their rounds to a particular species of plant. But, apart from its abundance, it cannot be urged that

F. W. Oliver, Trans. Linn. Soc., Bot., 2 Ser., Vol. VI, p. 376. The specimen is now in the Williamson Collection, No. 1486 a, Dept. of Geol., Nat. Hist. Museum.

² Ann. of Bot., Vol. XXIII, p. 92.

³ See Oliver & Scott, "Lagenostoma Lomaxi." Phil. Trans., B., Vol. 197, p. 214, footnote.

the purity of this pollen is a consequence of entomophily rather than of anemophily until extensive data are available of the contents of wind-supplied pollen chambers and collecting drops in natural environments. The mixed pollen in Ginkgo at Montpellier only informs us of a vicissitude incidental to existence in a botanic garden, whilst the plants of the Palæozoic grew in natural assemblages. It is easy to see why such data are not available. Their getting implies premeditated investigation at the right place and time. So long as botanists permit themselves to be encumbered with routine duties at urban centres during the season of vegetational activity so long will such ignorance continue.

The discovery that pollen may germinate in a foreign pollen chamber is not surprising in view of the many analogous records among Angiosperms of germination on foreign stigmas. the fossils the nearest parallel case occurs in a specimen of Physostoma elegans in Professor Bottomley's collection at King's College, London. In this section undoubted pollen grains of Physostoma have entered not the pollen chamber but the chink or sinus lying between it and the base of the whorl of tentacles which forms the free part of the integument in this seed. In this position the pollen grains have germinated to form bodies which may be sperms. matter was dealt with in my Physostoma paper.1

The question of the validity of the presumption that pollen present in the pollen chamber of a fossil seed really belongs to the plant is of some theoretical importance as it is apt to lead to the correlation of detached microsporangia.2 Seeing that this pollen is nearly always pure we may I think with reasonable safety continue to draw the accustomed inference until it shall have been established, for recent Gymnosperms in natural environments, that foreign pollen is liable markedly to preponderate. At the same time such conclusions are not infallible, for continuity is the final court of appeal, and pollen in a pollen chamber, even if it should have developed tubes, does not satisfy the requirements imposed by this

Annals of Botany, Vol. XXIII, p. 94, and Pl. VI, Fig. 30.

² Sahni, loc. cit., p. 150.

THE INTER-RELATIONSHIPS OF PROTISTA AND PRIMITIVE FUNGI.

(Continued from p. 168).

We prefer to regard the Proteomyxa as a generalised and synthetic group of Protista, derived from the Pantostomatineæ and comprising forms representing a series of lines leading up to various higher groups into the lower members of which these forms shade off in some cases by almost imperceptible gradations.

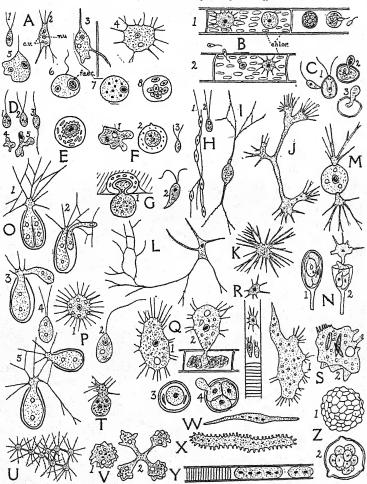


FIG. 4. PROTEOMYXA (in wide sense, see Text). A, Pseudospora lindstedtii Hartog; 1, flagellate zoospore; 2, young amœbula; 3, amœbula sending a pseudopodium into a fungus hypha; 4, full-grown amœbula; 5, 6, mature cells rounded off, protruding a flagellum before encysting; 7, division of nucleus into eight; 8, later stage in formation of zoospores. B, Pseudospora parasitica Cienk., parasitic in algal filaments: 1, in algal cell on left, a Pseudospora in the heliozooid

phase, and one rounded off, in cell on right division into zoospores; 2, infection of a filament by zoospores, amœbula and heliozooid phase. C, Colpodella pugnax Zopf: 1, an individual attacking a Chlamydomonas; 2, 3, after destroying the host, the parasite escapes in amceboid form, but later divides into flagellate individuals. D, Protomonas sp. Cienk: 1, 2, 3, different forms of zoospore; 4, 5, amcebulæ. E, Diplophysalis stagnalis Zopf, showing formation of endogenous cyst with spinose wall. F, Pseudosporidium brassanium Zopf: 1, amcebula; 2, cyst; 3, zoospore. G, Ectobiella plateaui de Bruyne: 1, parasite sending a pseudopodium into a diatom; 2, zoospore. H, Diplophrys stercorea Cienk.: six individuals united by fine pseudopodia to form a loose plasmodium; 2, zoospore. I, Biomyxa cometa Cienk. J, Arachnula impatiens Cienk. K, Pontomyxa flava Tops, L, Boderia turneri Wright. M, Dipłophrys (?) archeri Barker. N, Bursulla crystallina Sorokin: 1, stalked cyst; 2, rupture of cyst and escape of amœbulæ. O, Mikrogromia socialis Hertw. and Lesser: 1, individual undergoing longitudinal division (transverse division also occurs in this organism); 2, escape of one individual as a Mikrogromia form; 3, escape of one individual which later (4) becomes a zoospore; 5, two individuals formed by division, as in 2, remaining attached to form a young colony. P, Ciliophrys infusionum Cienk.: 1, heliozooid form; 2, zoospore. Q, Vampyrella spirogyræ Cienk.: 1, heliozooid phase; 2, same attacking a Spirogyræ cell; 3, endogenous cyst in which division occurs; 4, encysted individual divided into four amæbulæ of which one is escaping. R, Vampyrellidium vagans Zopf: four heliozooid individuals of different ages in an Oscillatoria filament. S, Leptophrys: 1, L. vorax Zopf, heliozooid phase; 2, L. villosa de Bruyne, amœboid phase. T, Nuclearia delicatula Cienk., heliozooid phase. U, Monobia confluens Schneider, plasmodium of heliozooid individuals. W, Gloidium quadrifidum Sorokin: 1, amœboid individual; 2, division into four. W, Gringa filiformis Frenzel. X, Enteromyxa paludosu Cienk., with numerous short pseudopodia along the vermiform body. Y, Endyonema polymorpha Zopf, multinucleate individuals (or plasmodia?) in an Oscillatoria filament. Z, Haplococcus sp. Zopf: 1, cyst, external view; 2, optical section of cyst, showing three pits and division of contents. Lettering :-chlor., chloroplasts of algal filament; c.v., contractile vacuole; fæc., fæcal vacuole; nu., nucleus.

It must be admitted that Zopf's division of Proteomyxa into Zoosporeæ and Azoosporeæ leads to the separation of forms which differ in little or nothing more than the presence or absence of a flagellate phase. The life histories of several of the genera are very incompletely known, and it may be noted that recent investigation of forms previously described as Azoosporeæ has resulted in the discovery of a flagellate phase. Partly for convenience, partly because on the whole it would appear that the Zoosporeæ include the more primitive forms of Proteomyxa, we shall take these first.

What we may take as the typical life history of the simpler Proteomyxa, that is, those which approach most closely to the Pantostomatineæ from which we assume the group to have arisen. and which indeed differ from such Pantostomatineæ as Mastigamæba or Dimorpha only in the predominance of the amæboid or heliozooid phase over the flagellate phase, is well seen in Pseudospora and its allies. In Pseudospora (Fig. 4, A, B) a cyst is formed which gives rise to a number of flagellulæ, but these after reaching the host (species of algæ or fungi) lose their flagella and become amæboid and later heliozooid and finally producing a cyst. A curious feature in Pseudospora lindstedtii is a return to the flagellate condition at a late period, a flagellum being protruded just before encystment (Fig. 4, A, 5, 6). In P. volvocis, recently investigated by Miss Robertson (1905), the amæboid or heliozooid form produces not only flagellulæ (flagellate zoospores) but also numerous minute zoogametes which fuse in pairs, the zygote after a time losing its flagella and becoming amœboid on reaching a Volvox colony into which it creeps. Except for the doubtful genus Chlamydomyxa, this appears to be the only case in which sexual reproduction has been

observed in Proteomyxa. Closely related to Pseudospora are several other genera which show the same general life cycle and differ from that genus and from each other in little except details of form and ornamentation of the cyst-among these are Colpodella (Fig. 4, C), Diblophysalis (Fig. 4, E), Pseudosporidium (Fig. 4, F), Ectobiella (Fig. 4, G), Aphelidium and others. In Ciliophrys (Fig. 4, P), the only stages known are a heliozooid form and a flagellate form into which the first passes, on withdrawing its radiating pseudopodia; no cyst or amœboid stage have been described, and if these do not occur we have in this genus an extremely simple Proteomyxan which differs from the Pantostomatinean genus Dimorpha only in the nonretention of the flagella in the heliozood phase. In Polysporella, described by Zopf (1885 b), the life cycle differs from that of other Proteomyxa in the fact that the contents of the cyst divide into from 4 to 16 portions, each of which becomes a resting spore or secondary cyst producing usually four flagellulæ; this genus may be regarded as leading to the Plasmodiophoraceæ or might indeed be included in that group. In another series of Zoosporæ small plasmodia are formed by the amæboid or heliozooid individuals becoming joined up by their pseudopodia, or fusing together. A simple type of this kind is Diplophrys stercorea (Fig. 4, H), which presents resemblances to the simpler colonial Foraminifera on one hand and to the somewhat isolated genus Labyrinthula on the other. In Protomonas (Fig. 4, D), which is otherwise similar to Colpodella, and in Gymnococcus and some other genera, plasmodium formation occurs by fusion of amœboid individuals. The genus Mikrogromia (Fig. 4, 0) may be provisionally included in the Zoosporeæ, though often placed among the lower Foraminifera; the body is covered by a simple membranous or gelatinous test open at one end, and division (frequently longitudinal, as in Flagellata) results either in the formation of two new individuals with branched (foraminiferoid) pseudopodia, which often become united so as to form a loose colony or in that of flagellate zoospores. The remarkable genus Chlamydomyxa, which might perhaps be included in the Zoosporeæ since it produces flagellate zoospores (or gametes), differs so much from other Proteomyxa that it will be best considered separately.

It will be noted that among the Zoosporeæ we have forms which present at any rate general resemblances to Heliozoa, Foraminifera and Mycetozoa. Similar resemblances to these and other groups of Protozoa are presented by various Proteomyxa in which no flagellate phase has been observed. Among the Azoosporeæ there are forms which show much the same general form and life history as certain Zoosporeæ but apparently produce no flagellated cells. Among the heliozooid forms (that is, forms in which the trophic phase shows a general resemblance to such Heliozoa as Actinophrys), Nuclearia (Fig. 4, T) corresponds to Ciliophrys in the Zoosporeæ; Vampyrella (Fig. 4, Q) to Pseudospora, though in some species a plasmodium is formed by fusion of several individuals; Leptophrys (Fig. 4, S) resembles Vampyrella but plasmodia are formed by fusion of the amœboid zoospores; Monobia (Fig. 4, U) has a plasmodium formed by union of the pseudopodia of several of the heliozooid individuals. Other forms (apart from Haeckel's " Monera" hardly any of which have been observed by any other writer), are amæboid and have affinities with the naked Rhizopoda (Gymnamæbida), e.g.,

Gloidium (Fig. 4, V), Gringa (Fig. 4, W). Others, again, resemble the simpler Foraminifera in having branched and anastomosing pseudopodia, e.g., Biomyxa (Fig. 4, I), life history unknown; Arachnula (Fig. 4, J), cysts formed; Pontomyxa (Fig. 4, K), reproduction by multiple fission; Boderia (Fig. 4, L), differing from the preceding genera in having a delicate membranous or mucilaginous investment from openings in which there protrude long branched pseudopodia and in producing cysts from each of which an amæbula emerges; Diplophrys archeri (Fig. 4, M), with a more definite envelope with a wide aperture at the two ends from which project the pseudopodia. Finally we have a number of forms in which plasmodia are formed by the fusion of amœboid zoospores, and which therefore seem to approach the Mycetozoa; examples are Enteromyxa (Fig. 4, X), Endyonema (Fig. 4, Y), Haplococcus (Fig. 4, Z), and Bursulla (Fig. 4, N). The last-named genus is practically a small Mycetozoan (Myxomycete), growing on dung (the other three genera just mentioned are parasites), with a stalked ovoid cyst or sporangium in which are formed 4 to 8 amæboid spores; these on emerging creep about, probably undergo division, and finally coalesce to form plasmodia which in turn give rise to a single cyst or a number of

cysts according to their size.

Two genera which may perhaps be included in Proteomyxa are Chlamydomyxa and Labyrinthula, formerly regarded as closely related but now known to differ in many important respects and indeed to bear a purely superficial resemblance to each other. Further work on both genera is very desirable—on Labyrinthula because its life history is very incompletely known, on Chlamydomyxa because such diverging accounts have been given by different observers. Chlamydomyxa (Fig. 5) the life cycle is divisible into two main phases. a free active stage in which food is ingested by means of pseudopodia and also obtained by photosynthesis, and an encysted stage in which spore formation occurs. In the free stage the organism is multinucleate, the protoplasm also containing chromatophores, contractile vacuoles, phloroglucin (?) particles functioning as reserve food material, and calcium oxalate crystals. According to most accounts. the protoplasmic body is much branched in a dendroid manner, with fine pseudopodia extending out into the water from the main branches, the chromatophores being confined to the latter while the stiff but flexible pseudopodia (which can be rapidly withdrawn into the general mass when the organism is disturbed) bear spindleshaped phloroglucin particles (those in the main mass of the body being rounded or ovoid) which have been termed "oat-like corpuscles." The chromatophores are apparently not symbiotic alga, as formerly supposed, since they have no cell-wall or nucleus but wholly resemble the ordinary chromatophores of plants, and they contain in addition to chlorophyll yellow-brown pigment probably similar to diatomin. Hieronymus (1898), who reinvestigated C. labyrinthuloides (discovered by Archer in 1875), states that the organism, as observed by him over a long period, never assumed this dendroid form at all, but the protoplasmic mass emerging from the cyst usually divided by simultaneous or successive fission into small uninucleate amæbæ (equal in number to the nuclei contained in the cyst) which after creeping about for a time passed into the encysted form, though sometimes this division remained in abevance during a feeding period. However, the account given by Hieronymus for the multinucleate encysted stage of *C. labyrinthuloides* agrees closely with that of Archer, and Hieronymus did once see a small specimen suspended in water with fine pseudopodia radiating in all directions; hence the discrepancy between the two accounts of the free stage may be explained either by supposing that Hieronymus was examining a different species or a related genus, or that his

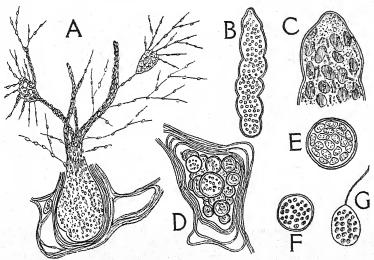


FIG. 5. Chlamydomyxa (A-D, C. labyrinthuloides; E-G, C. montana). A, part of organism in the free state, partially emerged from the lamellate cyst. B, cyst from hyaline leaf-cell of Sphagnum, constricted by the annular bands of the latter. C, part of a cyst, showing the chromatophores (shaded) and the phloroglucin granules (many of these arranged in chains), D, cyst with mature spores. E, early stage of spore formation—the cyst contents have divided up into young spores. F, spore, showing a nucleus at each pole, and numerous chromatophores. G, flagellula (gamete?) emerged from a spore. A-C after Hieronymus; D after Archer; E-G after Penard.

form may have been C. labyrinthuloides itself showing only early stages not previously observed, or this species may, like various other Proteomyxa (and other Protista), be polymorphic in its trophic or vegetative phase. After encystment the contents divide into 20 to 40 portions (secondary cysts, or spores), which in C. montana, according to Penard (1904), are binucleate and flagellate and may fuse in pairs. Penard suggests that Chlamydomyxa is related to the Mycetozoa, but its free stage cannot be regarded as a plasmodium, and from the facts available at present as to its life cycle it would appear better to place it among the lower Proteomyxa in the neighbourhood of Pseudospora, though its filose pseudopodia recall Mikrogromia and the lower Foraminifera, while in having numerous nuclei it resembles some of the Lobose Rhizopods like Trichosphærium as well as the Sporozoa. On the other hand, should more critical investigation establish the non-symbiotic nature of the chromatophores, the genus might well be regarded as related to the Brown Flagellata, some of which show amæboid trophic phases.

(To be continued).

REVIEWS.

SOME RECENT TAXONOMIC WORKS.

(1) Minnesota Trees and Shrubs: an illustrated manual of the native and cultivated woody plants of the state. By Frederic E. Clements, C. Otto Rosendahl, and Frederic K. Butters. Report of the Botanical Survey, IX. Demy 8vo., pp. xxi + 314. The University of Minnesota, Minneapolis, Minnesota; 1912.

(2) ROCKY MOUNTAIN FLOWERS: an illustrated guide for plant-lovers and plant-users. By Frederic Edward Clements and Edith Schwartz Clements. Pp. xxi + 392 (including 46 plates, many of them in colour). White Plains, N.Y., and New York City:

1914.

(3) REVISIONS OF SOME PLANT PHYLA. By [the late] Charles E. Bessey. Pp. 73, reprinted from the University Studies, Lincoln, Nebraska, Vol. XIV, No. 1; 1914.

(4) Dansk Ekskursions-Flora. Tredie udgave. 8vo., pp. xxvi + 330. By C. H. Ostenfeld and C. Raunkiaer. Copenhagen

and Christiania; 1914.

(5) FLORA OF THE VICINITY OF NEW YORK: a contribution to plant geography. By Norman Taylor. (Memoirs of the New York Botanical Garden, vol. V.) Pp. vi + 683; 1915.

THE first of the above books is the third of a series intended to familiarise students with the plants of Minnesota, Minnesota Alga and Minnesota mushrooms being its two predecessors. The book is copiously illustrated with text-figures, drawn chiefly from Minnesota specimens, though a few have necessarily been adapted from other works which are cited in the preface. The drawings are natural size, except where otherwise stated; and the majority were made by advanced students under the supervision of the authors. There are also a few "half-tones" made from photographs and an excellent frontispiece of Pinus strobus. The all-too-short introduction gives an account of the vegetative regions; and no p. xx there is a map in black and white showing the natural distribution of forest and prairie, the map being (as stated) adapted from Upham's Flora of Minnesota. There is also on p. xvii a phylogenetic scheme representing the authors' views of the relationships of vascular plants. From this scheme the authors appear to regard all Angiosperms as having arisen from the Ranales; and the three main lines of development end respectively with the Orchidales, the Asterales, and the Lamiales. A key to the genera occupies eight pages. The book generally is a systematic account of the families, genera, and species (with keys to the genera) of the trees and shrubs of the state and concludes with a glossary and an index. The work has been written with obvious care, and is an extremely useful contribution to botanical science. The arrangement of orders and families is that of Bessey (see 3, below).

(2) The second book, by Professor and Mrs. Clements, is an endeavour to present the materials of the flora of the Rocky Mountains in preliminary form "from the standpoint of the experimental ecologist" who, we are told, "is concerned primarily with the relationships of 'species' and their sub-divisions as an organic expression or measure of habitat differences, and of the

competitive relationships of the various formations."

The authors go on to express their opinion that "whatever the taxonomic value of the numerous segregates of the last decade or two, the fact that the binomial form conceals the relationship to the original species, and that the segregate itself is based not at all or only slightly upon habitat relations makes them of little value to the ecologist." The writer must confess that he is out of sympathy

with the point of view here adopted by the authors.

The book, we are told, is the forerunner of the long-promised one on the vegetation of the Rocky Mountains which has been "under way" since 1899. "The description of several hundred units [the authors' 'species'] were written in the field from a large number of individuals, whenever possible under different conditions." The arrangment of this as well as of the preceding book follows in general the Besseyan system of classification; but "the pines are placed at the end of the book quite frankly out of their proper position for reasons of convenience." A leading feature of the book is its illustrations. Many of these are in colour; and the rest are line drawings. The latter are drawn largely from herbarium material, and are (except in case of fruits, etc.) natural size. The coloured illustrations are by Mrs. Clements, and have with few exceptions, been made in the field. There can be no doubt that they enhance the appearance, interest and usefulness of the book very considerably. As in the case of "three-colour" reproductions generally, the greens are not very successful; but otherwise the reproductions are very pleasing, and demonstrate the skill and versatility of the talented authoress and artist.

(3) Some time has elapsed since the publication of Bessey's Synopsis of Plant Phyla (University Studies, Lincoln, Nebraska, vol. vii, no. 4). During the interval "many changes in the arrangement of the orders and families of several of the phyla" have been made; and "on account of their considerable number," the present paper, published but a short time before the author's lamented death in February last, has been issued as a whole, "so as to accomplish the revision of the original paper with as little confusion as possible." Professor Bessey thinks that the vegetable kingdom is "readily separable" into fourteen phyla; and no apology need be offered for citing the following interesting table and figures from page 1 of the paper under notice:—

Classes Families Species 2 1. Myxophyceæ 18 2,020 2 16 2. Protophyceæ 1.090 2 21 Zygophyceæ 7,000 3 26 4. Siphonophyceæ 1,260 3 5. Phæophyceæ 5 24 1,030 24 6. Rhodophyceæ 3,050 3 7. 29 146 64.000 Carpomyceteæ ... 2 7 65 16,600 Bryophyta 8. ... 2 Pteridophyta 3.800 9. 24 Calamophyta 10. 2 3 7 700 11. Lepidophyta ... 13 12. Cycadophyta 140 ... 2 9 400 13. Strobilophyta 300 32 ...132,500 14. Anthophyta 123 686 ...233,614 Total

Following the above table is a "key to the phyla of plants," and then we come to the main body of the paper in which the 4th, 6th, 7th, 12th and 14th phyla are revised: the remaining phyla are left therefore as they appeared in Bessey's original paper (cited above). The revision consists of a statement of the characters of each of the five phyla, and short characters of their contained classes, orders, and families. The revision of the 4th, 6th, 7th and 12th phyla occupies about 30 pages, and of the 14th ("Anthophyta"

or flowering plants) about 40.

A short statement of the chief features of Bessey's system of classification is here given, in so far as it relates to flowering plants. The usual division into monocotyledons and dicotyledons is made, the former being placed first; but the latter group "was probably the earlier, as it is now much the larger numerically. Indeed it is becoming more probable that the monocotyledons are to be regarded as a peculiar side branch which sprang from the primitive dicotyledons after the latter had become well established. Yet the monocotyledons have not developed to as high a rank in any of their orders as have some of the dicotyledons." The question of a possible polyphyletic origin of the monocotyledons is not mentioned. A very serious weakness in Bessey's treatment of monocotyledons is that his main sub-division of them is based on hypogyny and epigyny: hence the undoubtedly closely allied Liliaceæ and Amaryllidaceæ are widely separated, and the same is the case with regard to the Alismataceæ and the Vallisneriaceæ. The dicotyledons are also divided into two sub classes, the Axifloræ (or "axisflowers") and the Calycifloræ (or "cup-flowers.") contains the following orders:-Ranales (which includes such The former families as Saururaceæ and Piperaceæ in addition to such as Magnoliaceæand Ranunculaceæ) Malvales (which includes Ulmaceæ as well as Malvaceæ and the like), Sarraceniales, Geraniales, Guttiferales, Rhœadales, Caryophyllales (which includes Salicaceæ), Primulales (which includes Plantaginaceæ), Ericales, Ebenales, Polemoniales, Gentianales, Scrophulariales, and Lamiales. Calycifloræ contains the following orders:—Rosales (which includes the Casuarinaceæ)1 Myrtales, Cactales, Loasales, Celastrales, Sapindales (which includes Juglandaceæ, Betulaceæ, Fagaceæ, Myricaceæ, Julianaceæ, Proteaceæ, as well as Sapindaceæ, etc.), Umbellales, Rubiales (including Adoxaceæ), Campanulales and Asterales. The last-named order is equivalent to the Compositæ which Bessey sub-divides into as many as fourteen families. It ought to be stated that the two sub-classes Axifloræ and Calycifloræ are each split into two "super-orders," the super-orders virtually being polypetalous and gamopetalous respectively; and the Gamopetalæ as a distinct group disappears.

There are without doubt, many suggestive hints of affinity in Bessey's scheme; but in the writer's opinion the main divisions are artificial. This is seen particularly in the separation of the Liliaceæ from the Amaryllidaceæ, and (among the dicotyledons) of the separation of the "Nelumbaceae" and "Cabombaceae" from the "Nymphæaceæ." There would appear to be no likehood of Bessey's interesting arragement of plants ousting its more virile, old-world

Bessey adds that "this family, which has puzzled botanists from the first, is doubtfully placed here, on the theory that these plants are leafless relatives of the Hamamelidaceæ."

rivals in the struggle for existence. The paper concludes with a phylogentic chart, summarising Bessey's views of the relationships of the orders of his "Anthophyta" (or flowering plants.) It would have been a great convenience to students unfamiliar with this system of classification if the paper had been supplied with an index.

(4) Ostenfeld and Raunkiaer's "Pocket Flora" (as we should say in this country) is a very carefully arranged guide to the living vascular plants of Denmark. It is, of course, written in Danish; but botanical Danish should not give much trouble to botanists acquainted with Latin and German. Not only will the book be useful to any botanist travelling in Denmark, but it furnishes in small compass a ready means of comparing the British flora with that of Denmark. One can see at a glance, by comparing the British with the Danish species of a few well-chosen genera, the main differences between the two floras—the absence from Denmark of the British Arctic-Alpine species, (such as Juncus castaneus, J. biglumis, J. triglumis, J. trifidus, Luzula spicata and L. arcuata) and the British southern species (such as Juncus acutus and Luzula forsteri), and the occurrence in Denmark of central and eastern European species such as Juncus fuscoater, J. atricapillus, and Luzula nemorosa) which are absent from the British Isles. The absence from Denmark of the Arctic-Alpine species is, of course, very easily explained; but the other two classes represent a remarkable and interesting difference in the floristic phytogeography of the two countries.

(5) The fifth book deals with the vascular plants which grow near New York. "Taxonomy and nomenclature," the author states, "are considered only as fundamentals upon which the phyto-

geographical structure of the book has been reared."

An interesting phytogeographical introduction of thirty-seven pages is provided, dealing with the factors which affect distribution. Dealing with edaphic factors, which are always more important than climatic factors in the study of the flora or vegetation of a limited region, the author argues that a geological explanation is the only one which will account for the peculiarities of the "pinebarren flora;" and he gives a very suggestive account of the influence of recent geological changes of the district, and the resultant plant-migrations.

Raunkiaer's growth-forms (see Journ. Ecol., vol. I, 1913, pp. 16-26) are alluded to, and "may form the basis of a future study."

A long list of previously published local floras is given; and

there is a capital index.

With regard to the flora proper, occupying over six hundred pages, it is impossible for one unacquainted with the district to indulge in any detailed criticism. It should be stated, however, that the general impression is received that the work is very carefully done, and that botanists have here a thorough and detailed presentment of the species inhabiting the New York district. Previously published records, up to the end of 1913, have been utilised, though only sparingly, in Poaceæ (or Gramineæ), Cyperaceæ, Cratægus, Rubus, Rosa, and Viola, all of which are more or less "critical" groups in temperate North America. Native and introduced species are included in the general text, "besides many more, mentioned in notes, that are little more than waifs."

The arrangement is that of Engler and Prantl, the nomencla-

ture that of the New York and Washington botanists. nomenclatorial rules of the botanists of these eastern American cities differ from those laid down at the international congresses of Vienna (1905) and Brussels (1910). For one thing, priority is claimed by the former for genera as well as species, and this priority begins mechanically with the year 1753. There are thus no nomina conservata; and we have (to mention only a few of the numerous differences in generic names) Filix displacing Cystopteris, Tissa replacing Spergularia, and Uva-ursi displacing Arctostaphylos. These generic names involve further upheavals in the names of species and varieties. Fortunately, there appears to be no likelihood whatever that systematists in other parts of the world will ever adopt this point of view; and some day it may be realised that the tail should not wag the dog. Pteridium is cited as of Scopoli: but it does not seem to be realised that Pteridium Scopoli is the equivalent of, and is antedated by, Pteris Linn., and that Pteridium Scopoli is therefore a much bigger genus than Pteridium Kuhn. Duplicated names, such as Alnus alnus (= A. glutinosa), Hepatica hepatica (= H. triloba = Anemone hepatica), are used. The tendency to use small genera seems to the present writer to be carried too far, as, for example, in the separation of Batrachium from Ranunculus. However, when due allowances are made for matters on which there can obviously be legimate differences of opinion, it remains that the author has issued a book of very great merit.

It would be interesting to cite at some length the author's views on certain plants which are common to New York and the British Isles; but space forbids. It must suffice therefore to mention the case of Calluna vulgaris. This is treated "as an escape.....not recently collected." It appears to be the prevailing American opinion that Calluna is not indigenous in North America, but has been introduced there from Europe. The opposite view is usually assumed by non-American botanists.

C.E.M.

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AN ABNORMAL STEM OF LONICERA PERICLYMENUM.

By CHRISTINE E. BURGESS, B.Sc.

[WITH TWELVE FIGURES IN THE TEXT].

A N abnormally developed stem of Lonicera Periclymenum was put into my hands. At first sight it was quite unlike a normal shoot, but there was very little departure from the usual type of anatomy beyond displacement. The specimen appeared, with two others of similar construction, as the only peculiar branch on the parent plant.

The normal shoot bore whorls of leaves, either two or three at each node. An interpetiolar ridge was formed by the union of adjacent leaf bases at the node. In the axil of every leaf a bud or branch was found (Fig. I).

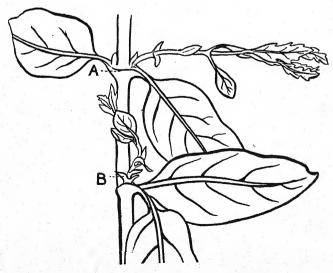


Fig. I. Normal Stem of Lonicera Periclymenum. A, interpetiolar ridge. B, axillary branch.

The lowest node on the abnormal specimen bore a pair of opposite leaves with an interpetiolar ridge on one side of the stem. This opposite arrangement was not retained at the second node, where two leaves, joined by a commissure, were closer together on one side of the stem than on the other. The following three leaves arose almost at one level and were united by a ridge. Above this region the leaves occurred singly at each node, placed on one side of the stem only. They were connected by a vertical ridge and inserted vertically or obliquely instead of in a horizontal plane. The buds showed a tendency to lateral and downward displacement, being on the left side of their respective leaves. Distinct spiral striations traversed the stem in a clockwise direction toward the apex (Fig. II).

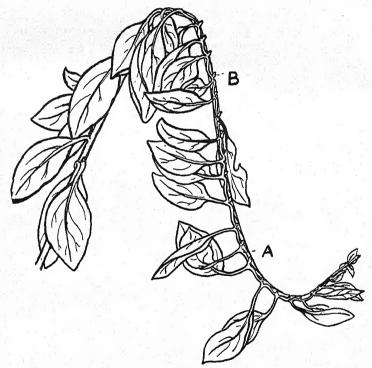
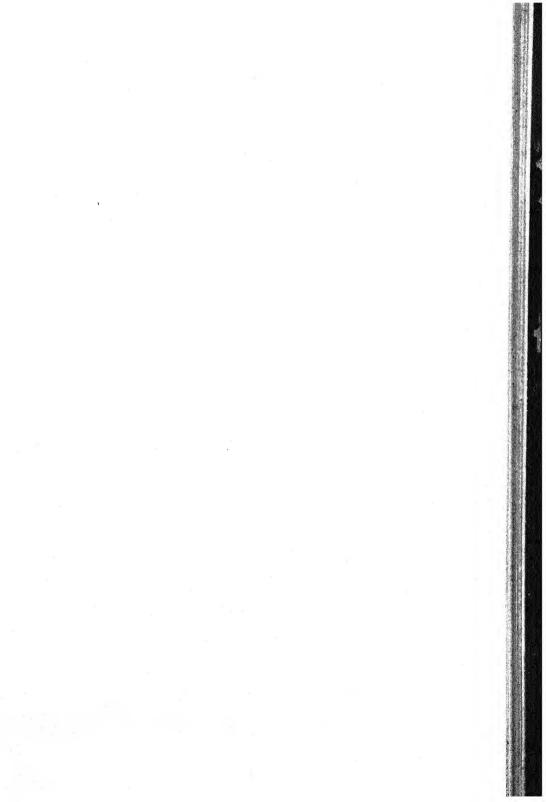
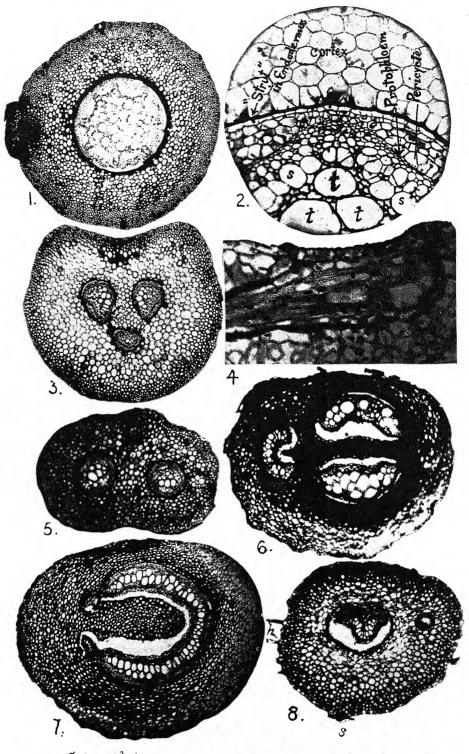


Fig. II. Abnormal Stem of Lonicera Periclymenum. A, interpetiolar ridge. B, bud.

Anatomy of the normal branch.

The arrangement of the vascular tissue in the normal stem was of a usual type. A complete cylinder of secondary vascular tissue surrounded the pith. Immediately below the point of



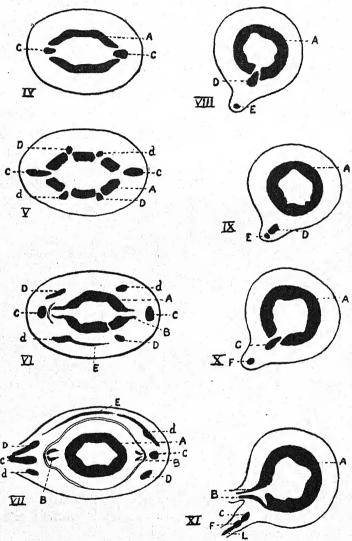


B. Sahni phot.

_SAHNI — NEPHROLEPIS.

An Abnormal Stem of Lonicera Periclymenum. 235

insertion of each leaf, a vascular strand, the median leaf trace, departed from the stele, leaving a gap in the central cylinder (Fig. IV). At a slightly higher level two lateral strands left the stele, one on either side of the gap left by the median trace, and separated from this by part of the vascular tissue of the stem (Fig. V).



FIGS. IV-XI. Diagrammatic Sections through a Node of the Normal Stem, in order from below upward. A, stele. B, vascular supply to bud. C, median leaf trace. D, left lateral leaf trace. d, right lateral leaf trace. E, interpetiolar commissure. F, ridge down side of stem. L, vascular tissue of leaf.

The three traces to the leaf took an oblique upward and outward course through the cortex, entered the petiole side by side and fused at a little distance from its base (Fig. VII).

Before leaving the stem, however, the neighbouring strands belonging to opposite leaves were joined by a narrow horizontal vascular commissure which passed through the ridge formed by the united leaf-bases. The bud supply passed off at about the same level, two strands of vascular tissue becoming dissociated from the main cylinder of the stem immediately on either side of the median leaf gaps. These strands passed out as two bundles to each bud (Figs. VI and VII).

Anatomy of the abnormal branch.

Node 1 (lowest on the stem). At the lowest node two leaves arose opposite one another, bearing buds in their axils and united by a ridge round the stem on one side only.

The vascular supply to both leaves did not arise at the same level. The left lateral trace to one leaf was separated from the main vascular cylinder just below the node. At a slightly higher level the median trace passed off followed by the bundles to the bud. No second lateral strand appeared, and the commissural bundle was absent.

The bundles to the second leaf at the node arise in the following order on proceeding up the stem:—left lateral leaf trace, median trace, right lateral leaf trace and bundles to the bud. The strands to the leaf passed separately into the petiole. The commissural bundle was again absent.

Node 2 (leaves 3 and 4). The two leaves at this node appeared to be at the same level but were not opposite to one another. Their bases were united round one side of the stem.

The vascular tissue of the two leaves joined that of the stem at slightly different levels, and in both instances, showed the same arrangement as appeared in the upper leaf at the first node.

Nodes 3-5 (leaves 5-7). The three succeeding leaves, five, six and seven, arose at intervals round the stem, each a little above the preceding one. The three were joined by a narrow ridge of tissue on the outside of the stem. They were attached somewhat obliquely, thus pushing the buds to one side. The structure was like that in leaves two, three and four, but for the fact that the first lateral and the median trace to each leaf joined while still in the stem. As before, there was no vascular supply to the ridge.

Node 6 (leaf 8). No commissure was present between leaves seven and eight, but the eighth leaf formed the first of a series extending to the apex of the stem, arising singly at each node, and joined by a commissural ridge. As regards internal structure, the sixth node was identical with the previous one.

Node 7 (leaf 9). All leaves from the ninth onward were on the same side of the stem (Figs. II and III).

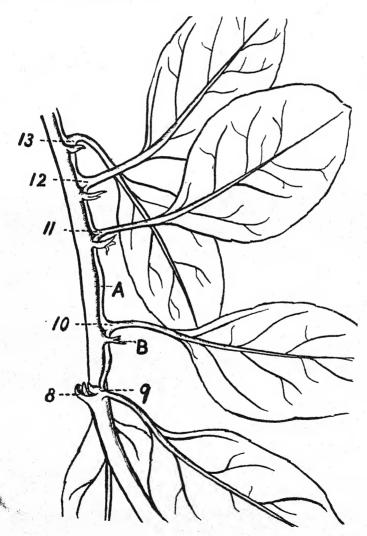


Fig. III. Part of Abnormal Stem of Lonicera Periclymenum. The figures refer to the number of the leaves beginning at the bottom of the stem.

At the seventh node a change in anatomy occurred, the two bundles to the bud leaving the stem below the right lateral trace to the leaf. Also these bud bundles both passed out on the left side of the median trace, though springing from either side of the gap left by this leaf trace.

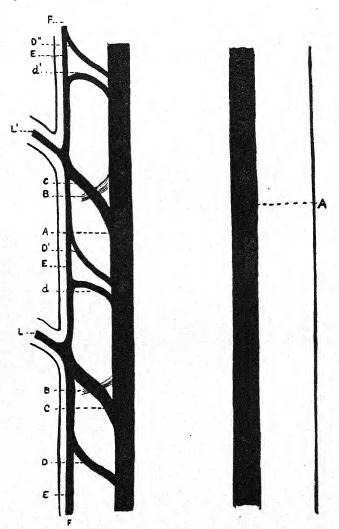


Fig. XII. Diagrammatic Longitudinal Section through Nodes 15-17 of Abnormal Stem. A, stele. B, vascular supply to bud. C, median leaf trace. D, D', D', left lateral leaf traces to leaves 17, 18 and 19 respectively. d, d', right lateral leaf traces to leaves 17 and 18 respectively. E, commissure uniting vascular tissue of adjacent leaves and completing the tissue of the ridge. F, ridge bundle. L, L', vascular tissue of leaves 17 and 18 respectively.

Node 8 and onward (tenth and subsequent leaves). At the region of the tenth leaf a vascular strand appeared, for the first time, in the vertical ridge joining the leaves. This bundle continued up to the apex of the stem. From this point upward the structure, both at nodes and internodes, remained invariable. Thus the portion of the stem below this may be regarded as a transitional region from the ordinary stem structure.

The following is the manner in which the ridge bundle was formed. The first or left lateral leaf trace, on leaving the central cylinder, took an oblique course upward and outward (Figs. VIII and IX). Whilst still in the cortex it was joined by the median leaf trace about the level at which the bud bundles arose from the stele (Fig. XI). The bundle formed by this fusion continued vertically upward through the outer ridged region of the cortex and part left the stem, as the bundle of the leaf, at a slightly higher level. The remainder of the strand continued upward in the ridge and was joined by the second or right lateral leaf trace. The ridge bundle then passed upward through the internode and was subsequently joined by the three traces to the next leaf.

The same type of structure was found in all leaves at higher regions of the stem.

The three strands to each leaf passed out from the stele at different levels and took part in the formation of the ridge strand, which was continuous through nodes and internodes (Fig. XII). A single bundle was given off from this to each leaf.

The bundles to the bud arose just above the point of origin of the median leaf trace, and slightly above this the tissue to the leaf left that of the ridge.

SUMMARY.

The abnormal specimen of Lonicera Periclymenum bore leaves singly at each node. These were obliquely inserted, and all arose from the same side of the stem (Figs. II and III). The buds showed lateral and downward displacement, being situated on the left side of their respective leaves.

A vertical ridge passed down one side of the stem connecting the leaf bases (Fig. III). The stem showed spiral striations.

A cylindrical stele traversed the stem from end to end. From this, three vascular strands, situated vertically above one another, passed out obliquely at every node.

These united with and formed part of a vertical bundle traversing the centre of the interpetiolar ridge (Fig. XII).

A single strand from this passed outward into the petiole at each node, about the level at which the median leaf trace left the stele. Just above this level, two vascular strands from the central cylinder entered the bud.

All the vascular strands present in the normal stem had their counter-parts in the abnormal specimen. That their position, with regard to the central stele should have been modified in connection with the changed direction of leaf insertion was to be expected.

It was interesting to find, however, that this displacement was almost the only alteration from the normal stem structure, and that no really radical rearrangement of structure accompanied the marked deviation from the normal mode of development of the shoot.

It is clear that in this example, the hereditary characters of the internal structure have escaped serious disturbance such as perhaps might have been looked for in a shoot so aberrant in external features.

CARBON ASSIMILATION.

A REVIEW OF RECENT WORK ON THE PIGMENTS OF THE GREEN LEAF AND THE PROCESSES CONNECTED WITH THEM.

By Ingvar Jörgensen and Walter Stiles.

PREFACE.

In these articles, a considerable quantity of work has been done in recent years, and a mass of fresh knowledge has been obtained. Much of the information thus afforded is not very easily accessible, and to those not actually engaged on work on the subject a considerable time is necessary to disentangle the essential facts from unessential details.

We have thought therefore that a review of the recent literature of the subject, in which the character of the involved problems is indicated, would be of interest.

CHAPTER I.

Introduction: Fundamental Principles.

The elements contained in the plant are such as are always present in ample quantity in air and soil, but in the plant they exist in compounds possessing greater energy than the simpler substances in the surroundings.

The fundamental characteristic of the green plant is that during its life it produces these compounds of greater energy from simple compounds, the energy required for this being obtained from the radiant energy of the sun.

One of the chief elements thus built up into the plant is carbon, which is provided by the carbon dioxide of the air. It is in this sense, and this only, that we use the term carbon assimilation. It is with various aspects of the complex processes involved in this that we shall deal in these articles.

In attempting to summarise the subject, the use of terms such as photosynthesis, photolysis of carbon dioxide, etc., are confusing, since each of such terms indicates a definite theory of the nature of the processes; and our main object is rather to emphasise the complexity of the subject, than to suggest or support any single theory.

The processes of carbon assimilation are dependent upon the transformation of the sun's radiant energy into chemical energy. Now we know a good deal about the relations between heat, electrical and chemical energy, but unfortunately for our purpose little is known concerning the relations between radiant energy and chemical energy. Yet the connection between radiant and chemical energy is most important, for upon it all life depends.

The very great importance of this aspect of the subject is perhaps not completely realised, nor how necessary the development of our knowledge of this relationship may be for future generations. We may, perhaps, then be justified in giving a few figures to indicate its importance.

It is, of course, owing to the sun's energy now stored in coal, and transformed from radiant to chemical energy by plants ages ago, that our present well-developed industrial civilisation is largely due. It is interesting then to enquire into the quantity of such energy there is available on the earth and the time we are likely to take to use it.

Naturally, such calculations are rather uncertain; we may however quote a recent one due to Gibson. According to this estimate the quantity of coal in the earth is 4×10^{12} tons. In 1905 there were mined 9×10^8 tons, in 1910 11×10^8 tons. If one assumes the consumption of coal to increase at this rate, all the coal will be used up in about 350 years. But of course long before that period has elapsed coal will be difficult to get, and consequently scarce and expensive and some other supply of energy will be necessary if an industrial civilisation such as ours is to continue.

Economy and the production of more efficient engines may enable the energy of coal to remain available for a somewhat longer period, but this would only postpone and not solve the problem. Moreover, probably there is not a great deal to be done in this direction. Petrol is a better source of energy than coal in regard to its efficiency, for a petrol motor transforms 35% of the energy of the petrol into useful work, whereas a steam engine only transforms from 10% to 16% of the energy of coal into useful work. But petrol production is only about 5% that of coal, and although we know nothing very certain about the amounts of petrol in the world, petrol is not very likely to replace coal as our principal source of energy.

Other sources of energy available for our use are waterfalls, winds and waves and tides. Winds and waves are of too unstable a character for industry to be based on them. Tides form a more regular source of energy, but are scarcely suitable for general use. In waterfalls, on the other hand, we have a large source of energy of which only a small fraction is utilised at present. It is estimated that waterfalls will give at least 200 million horse power while only about 100 million horse power is required for industry at present. Nevertheless, having regard to the present rate of increase of industry and considering that a proportion of the energy of waterfalls will not be available for use it would seem clear that some means of utilising the sun's energy such as the plant is able to do, will have to be developed if our civilisation is to continue. It is to be noted that all our sources of energy except the tides are derived from the sun's rays, and that in the case of coal and probably of petrol we are using energy which has been transformed from radiant energy by the agency ultimately of plants.

It has been estimated that the vegetable material formed each year by plant growth would give as much heat as 14×10^9 tons of coal, eleven times as much as the present consumption. But of course a good deal of such vegetable matter is used as food for animals and as building material.

However, of the total radiant solar energy only about 0.5% becomes stored up in the plant, and only a small part of this could be utilised. So the only solution of the energy question of the future appears to be in transformation of the sun energy which at present is so largely wasted.

The preceding figures, though very approximate, show the importance of the storing up of energy in the plants of the past and also of the present.

Part of the work of the plant physiologist must be to get a clear insight into the processes by which sun energy is stored up, not merely that by so doing plant cultivation shall be made as efficient as possible and agriculture made a real plant industry, but also that by clearing up these problems in the plant, a way may be opened for allied sciences, pure and applied, to find methods by which it will be possible to utilise or transform sun energy directly.

When æther vibrations in the form of light pass through matter the system can become affected in different ways.

- 1. The temperature of the body may be raised: the light energy is converted into heat.
- 2. The vibrations may give rise to changes of a chemical nature.

The first of these is a very general phenomenon. Most substances can change the energy of æther vibrations into heat. The extent to which this takes place depends on the nature of the substance, the thickness of the absorbing layer, and the wave-length of the light.

On the other hand, the chemical effect of light takes place only in exceptional cases. These constitute the so-called photochemical reactions. They are of the greatest interest, for they involve the conversion of æther vibrations into chemical energy.

Only during the last ten or fifteen years have investigations told us something about these photochemical reactions, and in spite of much uncertainty several facts have now become definite. Our intention is to draw attention to these facts, which deserve to be more generally known by plant physiologists than is generally the case. Above all we want to emphasise the fact that transformation of light energy into heat energy and of light energy into chemical energy are two essentially different phenomena. Although in the organisation of the plant these two phenomena may be connected and inter-related, yet the basis of our enquiries into carbon-assimilation should be that carbon assimilation consists of photochemical reactions, the main feature of which is that radiant energy from the sun, by means of chlorophyll in the plant, is transformed to chemical energy.

We propose to commence by giving an account of the main facts that recent investigations have made clear about the pigments in the plant, before considering the processes which may possibly occur and the factors influencing those processes.

CHAPTER II.

The Pigments of the Leaf.

A. GENERAL REMARKS.

It is necessary to review the present knowledge of pigments in the leaf before discussing the actions taking place there, more particularly as this knowledge has been considerably increased during recent years by the researches of Willstätter and his coworkers, and as the results of these researches do not appear as yet to have penetrated very deeply into the botanical world.

Willstätter's researches have extended over a period of more than ten years, during which time he has been assisted by many expert chemists, working under conditions which have enabled them to conduct experiments on a properly large scale. The result is that the chemistry of chlorophyll has been made at least as clear as that of any other plant substance, and there is every reason to hope that in applying the experience of Willstätter and his colleagues to experiments in plant physiology, great progress will be made.

Besides working out the chemistry of the leaf pigments and isolating them, Willstätter has made a large number of analyses of pigments from various species of different families, from plants growing under different ecological conditions, and from plants collected at different seasons and at different times of day.

The main facts derived from Willstätter's researches are that the chloroplasts contain four pigments, two green and two yellow These are:—

- Chlorophyll component a, C₅₅H₇₂O₅N₄ Mg, blue black in the solid state, green blue in solution.
- 2. Chlorophyll component b, C₅₅H₇₀O₆N₄Mg, green black in the solid state, pure green in solution.
- 3. Carotin, forming orange red crystals of the composition $C_{40}H_{56}$.
- 4. Xanthophyll, forming yellow crystals of the composition $C_{40}H_{56}O_2$.

It was found that these pigments were identical in all plants examined. The chlorophyll always contained 2.7% of magnesium, which is the only metal present in its ash. Neither iron nor phosphorus is present.

In fresh leaves these four pigments were found in about the following quantities:—

Chlorophyll a	•••	·	2	parts	per	1000
" b	•••		3	"	,,	1000
Carotin	•••	•••	16	**	95	1000
Xanthophyll	100		1	••		1000

In the chloroplasts these pigments are also mixed with various colourless substances; fats, waxes and salts of fatty acids. Thus in an alcoholic extract of dried leaves chlorophyll is accompanied by about six times its weight of other substances.

Willstätter has worked out methods for freeing chlorophyll extracts from these accompanying colourless substances, and also methods for isolating each of the four pigments. In all that follows, when we speak of chlorophyll we refer to the green pigments freed from the yellow ones.

In thus being able to obtain pure pigments a very great advance is made. All the earlier experiments on the reactions taking place in the green leaf were made with extracts, such as alcoholic extracts of leaves, which contained many substances besides the pigments.

Yet a further complication becomes obvious from Willstätter's investigations, and this is also a fact which has not yet received its due attention in physiological researches. Moreover it is a fact not only important in this branch of plant physiology but in all cases where plant substances are extracted and purified. This is that by the methods of extraction the state of matter in which the substance generally exists may be altered. For this reason it may become difficult to draw conclusions from the behaviour of the extracted substance as to the function of the substance in its natural condition in the plant.

From Willstätter's researches it is clear that solvents which dissolve the pure extracted substance do not extract the substance from the dried leaf. For instance, the pure pigment is readily soluble in acetone, ether and benzol. If the dried powder of nettle leaves is placed in pure acetone it can remain there for half an hour without the acetone becoming at all coloured. But if a little water is added the colour immediately becomes intensely green. Neither ether nor benzol becomes coloured quickly when powdered nettle leaf is added. Yet both are immediately coloured strongly green when a few drops of water are added. This behaviour of chlorophyll suggests that chlorophyll in the leaf is in a different state of matter from extracted chlorophyll.

The extracted pigment is soluble in petrol-ether as long as it

is mixed with accompanying oils, waxes, etc., but petrol-ether does not extract at all from dried leaves, so it is feasible to suppose that the chlorophyll in the chloroplast is in the colloidal condition, that water added to the pure organic solvents dissolves the mineral substances in the leaf, and the salt solution so formed alters the colloidal condition of chlorophyll in the chloroplast and makes it easily soluble.

In this connection it should be pointed out that the pure organic solvents can extract the chlorophyll from fresh leaves, as there is of course, abundant water present in them.

Support for this assumption is given by the fact that colloidal solutions of chlorophyll in water made up from the pure extracted pigment behave in a similar way to the dried leaf powder. Thus if a colloidal solution of chlorophyll is mixed with ether, the ether remains colourless, but if a little salt solution, for instance, a solution of calcium chloride or calcium nitrate, is added, on shaking the ethereal layer becomes coloured green. The salt solution has precipitated some of the chlorophyll from its colloidal condition and it is now easily soluble in ether.

In regard to the actual state of chlorophyll in the leaf there has been some difference of opinion. Arnaud (1885) supposed that capillary forces kept the chlorophyll back in the leaf, and Willstätter himself at one time assumed that chlorophyll in the leaf was present in the form of adsorption compounds with colloids. Similarly Tswett (1901) held that the pigment was bound to the skeleton of the chloroplast by molecular adsorption. Recently Palladin (1910a, 1910b) suggested that the chlorophyll is present in the leaf in a state of chemical combination, particularly with the so-called lipoid substances, and he shows that the use of solvents for extraction could be explained by their dissociating power in regard to the adsorption compound.

Willstätter's present opinion is that the chlorophyll in the chloroplast is present in a colloidal mixture, and there appears to be a good deal of experimental evidence in support of this view, even if it may have to be slightly modified when we have more experimental knowledge of the kinetics of the physiological processes involved.

We may mention briefly some other reasons for the assumption that chlorophyll is present in the colloidal condition. There is first evidence derived from spectroscopic examination. According to Tswett (1910) and other writers the absorption bands in the spectrum of the living leaf are displaced towards the red end of the spectrum as compared with the bands in the spectrum of extracted chloro-

phyll. Herlitzka (1912) has shown that the spectrum of living leaves agrees with that of colloidal chlorophyll solutions while both differ in the same way from the spectrum of true chlorophyll solutions. Willstätter's own experiments confirm the observations of Herlitzka. He made measurements of the bands in the spectrum of leaves of different plants and found them to occupy the same positions as the absorption bands of the spectrum of colloidal solutions of pure chlorophyll a.

Again the condition of the chlorophyll in fresh leaves is altered if the leaves are plunged in boiling water. After such treatment the chlorophyll is much more easily extracted. Microscopic examination shows that the chloroplasts are deformed as a result of such treatment, they are displaced from the normal position in the cell and diffusion out from them of chlorophyll follows almost immediately. Externally the leaves change in colour to a deep Spectroscopically this change in colour is shown to be accompanied by a displacement of the absorption bands towards the violet end of the spectrum so that they occupy practically the same position as those in the spectrum of a chlorophyll extract. This is explained at once on the view that the chlorophyll has changed from a colloidal to a true solution and is now dissolved in waxy substances which have become liquid as a result of the alteration of temperature. As would be expected, pure acetone and ether easily extract the pigment from a powder made from leaves previously steeped in boiling water.

It is worth mentioning that if fresh nettle leaves are treated with acetone or other solvents, and are then examined spectroscopically when they have become deep green but before any pigment has diffused out of the tissues, the same bands in the spectrum are observed as with the spectrum of the extract. It is thus possible to obtain within the leaf tissue a solution of the same kind as that obtained by extraction.

The various chlorophyll samples obtained by Willstätter by different methods of extraction are identical, whether obtained from fresh leaves, or from leaves put in boiling water, or from dried leaves. They showed no difference in chemical composition, solubility or optical properties.

While in the higher land plants examined the same four pigments are always present, and the ratio of the quantities in which the four are present does not vary very much, Willstätter found a somewhat marked variation in the green algæ, and a very different state of affairs in the brown algæ.

The green alga examined was Ulva luctuca. Here were found

the same four pigments as are present in higher plants, but the alga is comparatively richer in chlorophyll b and also contains, relatively to the chlorophyll, more of the yellow pigments than is present in the green leaves of land plants. Willstätter gives the following table for the pigments of Ulva, the numbers representing parts per thousand of fresh thallus:—

Chlorophyll a	•••		V	0.16
" b	•••	•••	•••	0.12
Carotin	•••	•••	•••	0.02
Xanthophyll	•••			0.06

The brown algæ stand of course in great contrast to the green algæ and higher plants as far as their external appearance goes in the matter of colour, and many views have been held in regard to the presence of pigments causing this colour. Thus Cohn (1865, 1867) supposed the cells of the Phæophyceæ contained a brown pigment called phæophyll nearly allied to chlorophyll. Molisch (1905) supported this view. In these brown forms he supposed the only pigment present to be a brown chlorophyll derivative which changes easily into ordinary chlorophyll when the thallus is immersed in warm air or water or is treated with organic solvents. Potassium hydroxide reacts with chlorophyll to produce a brown derivative which easily gives rise to green compounds, and with this brown derivative he compares phæophyll.

The theory generally taught in this country, which is the one held by Tswett (1906, 1910) and Czapek (1911), is that chlorophyll is present in the plastids of the brown algae but that its presence is masked by yellow pigments. The well-known class experiment of putting the thallus of a brown alga in boiling water which results in an immediate change of brown to green, is usually explained by supposing the brown covering pigment to be extracted by the water. Tswett suggests as an alternative explanation the alteration of the yellow pigment.

The completion of the proof that chlorophyll is actually present in the brown algæ has been made by Willstätter and Page (1914). These workers in dealing with the phæophyll theory of Cohn and Molisch show that if the algæ contained a pigment similar to that produced by the action of potassium hydrate on chlorophyll it would give different derivatives when subjected to different treatments, but this is not the case.

A second argument against Molisch's view is to be found in spectroscopic examination of the pigments. The brown chlorophyll derivatives give a spectrum quite different from that of chlorophyll, there is no absorption in the red, but strong absorption in the green

and violet. The spectrum of the brown algal thallus on the other hand is not at all like this, but is not much different from that of the green leaf. On putting into boiling water a change in the spectrum is observed similar to that observed in the case of the green leaf and this can be explained in a similar way by supposing a change in the chlorophyll from the colloidal condition to a solution in fats and waxes.

A microscopic examination of the thallus before and after treatment with hot water confirmed other lines of evidence.

As regards the composition of the pigments in the brown algosome workers, including Tswett, have supposed a third chlorophyll to be present; Tswett, for example, speaks of chlorophyll γ . Willstätter, however, could find no sign of such a substance when he treated fresh brown algo with cold solvents. But he has obtained this third chlorophyll derivative from stale or dried thallus. It is clear that the chlorophyll of the brown algo changes on standing, and the pigment is unstable in the dried plant.

The result of Willstätter's researches on the pigments of the brown algæ is to show that the same pigments are present in their plastids as in the chloroplasts of the green leaf, and that a third yellow pigment, fucoxanthin is present in addition, a pigment with the formula $C_{40}H_{56}O_8$. The green pigment is nearly all chlorophyll a; only traces of chlorophyll b were found. Willstätter gives the result of analyses of Fucus, Dictyota and Laminaria. The yellow pigments are much more abundant than in green plants. Instead of being present in the molecular ratio of 3 to 5 of green to 1 part of yellow pigment as in higher plants, the ratio is here more nearly 1 to 1.

Willstätter gives the following figures as the result of his analysis of Fucus pigments:—

Chlorophyll			•••	•••	0.503
(nearl	y all a,	not more	than	5% b).	
Carotin	***				0.089
Xanthophyll		•••	•••		0.087
Fucoxanthin		•			0.169

These numbers represent parts per 1,000 of the fresh thallus. The molecular ratios are:—

Chlorophyll	•••			3.64
Carotin		***	•••	1.08
Xanthophyll	***			1.00
Fucoxanthin		•••		1.75

In the following sections of this chapter we propose to deal more in detail with the chemistry of the pigments, their method

of extraction and variations in their amounts. It must, of course, be understood that anyone wishing to obtain first-hand knowledge of these aspects of the subject must consult Willstätter's book (1913) or his original papers referred to therein. Most of the information given in the succeeding sections of this chapter is due to Willstätter and his co-workers. It is impossible to offer any criticism of the methods or the results of Willstätter, and in many cases in the following we have simply had to quote him without comment.

In view of the information given by Willstätter's researches it becomes unnecessary and would only be confusing, to enter into any discussion of the different results obtained by other continental investigators of this subject such as Hoppe-Seyler (1879, 1880, 1881), Gautier (1879) and Stoklasa (1907, 1909, 1913). It is sufficient to indicate that their results now appear due to their imperfect methods of extraction.

The difficulties of isolating chlorophyll, partly because it changes so easily to other substances, and is so soluble in many solvents, has had the result of producing a very voluminous literature, but not even the most elementary questions had been solved before Willstätter's researches. Thus it was not known whether there was one chlorophyll substance or more than one and as recently as 1906, Étard claimed to have found in one plant a whole series of different chlorophyll pigments, and an unlimited number of chlorophylls from different plants. Also the elementary questions of analysis had not been solved. It was not even known which elements were contained in the chlorophyll molecule.

Now, owing to Willstätter's work, which is undoubtedly one of the most brilliant achievements of organic chemistry, our knowledge of the chemistry of chlorophyll is as complete as, or more complete than, that of any other plant substance. His researches have therefore cleared the way for a vast amount of plant physiological work of the greatest importance. It seems impossible that this unique work of Willstätter and his co-workers should not influence and stimulate work in plant physiology, and it is surprising how little this work has influenced plant physiological research so far. Thus, in some recent work (Ewart, 1915) where it is contended that Willstätter's methods of extraction have been followed, it would have been more convincing if the author of the paper had stated what chemical tests he applied to test the purity of his extracted pigment.

(To be continued).

THE ANATOMY OF NEPHROLEPIS VOLUBILIS J.Sm.,
WITH REMARKS ON THE
BIOLOGY AND MORPHOLOGY OF THE GENUS.

By BIRBAL SAHNI.

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[WITH PLATE IV AND SEVEN FIGURES IN THE TEXT].

I. INTRODUCTION.

THE subject of this paper is a description of a species of Nephrolepis (N. volubilis J.Sm.)¹ collected near Kuala Lumpur, Federated Malay States, by Mr. F. T. Brooks during 1914. In spite of its many interesting features, this plant does not seem to have been previously investigated.² The enormously long stolons which enable the young plants arising on them to climb trees to a very considerable height, the entire absence of roots on these lateral plants, and the presence on them of coiled tendril-like stolons which suggest contact irritability, are features of biological interest which seemed worth investigating; the mode of branching of the stolons and the structure of the lateral plants were followed out in some detail. Unfortunately, no part of the mother-plant was available, nor is the latter represented in any of the specimens at the Kew Herbarium; each contributor seems to have collected only a portion of the long stolon bearing some lateral plants.

It may be mentioned that several of the systematic authors who have described this plant refer to the stolon as if it were the main axis of the plant.³ I am indebted to Mr. Boodle for the discovery of this error.

During the work, comparisons with other species of Nephrolepis were frequently necessary, and a few of these observations are included below. These would have been inaccessible to me had it not been for the kindness of Dr. Stapf, who granted me the privilege of dissecting dried material from the Royal Herbarium,

¹ Christ, "Farnkräuter der Erde," p. 288, 1897; Clarke, Trans. Linn. Soc., Bot. II, 1879, p. 541, pl. 78. Synonyms are *N. radicans*, Kuhn, Ann. Mus. Bot. L.B. iv., 285; *Polypodium radicans*, Burm. (oldest name).

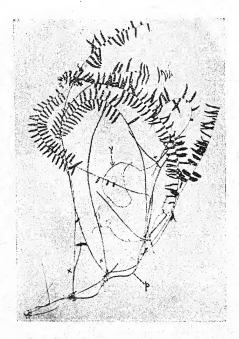
² The only anatomical observations which can refer to this plant are in a paper (Ann. Sci. Nat. V, t. xii, 1869) by Trécul, called "Remarques sur la position des trachées dans les Fougères." The author, in a footnote on p. 245, alludes to the outstanding anatomical features of a fern which he elsewhere (Ann. Sci. Nat. V. t. x, 1869, p. 351) regards as probably a Nephrolepis, but which he was unable to identify. His brief account, so far as it goes, agrees largely with that set forth below, and it is likely that his plant was the same.

³ Clarke, 1.c.; Christ, 1.c.; Diels in Engler u. Prantl, Nat. Pfl.; van A. van Rosenburgh, "Malayan Ferns," 1908, p. 161.

Kew, and of Mr. R. I. Lynch, M.A., Curator of the Cambridge Botanic Garden, who helped me with fresh material. To both my sincere thanks are due. I have also to thank Mr. Ridley and Mr. C. H. Wright for help in identifying the specimen of N. volubilis.

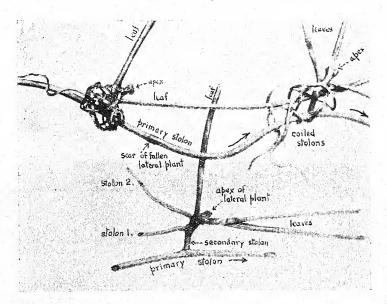
II. METHODS.

Special mention may be made of the way in which the diagrams in Text-fig. 4 were obtained. The stele of the primary stolon being only loosely attached to the cortex, it is easily dissected out. When freshly removed it is cylindrical, but on being left to dry up, it assumes the shape of a fluted column of which the ridges correspond to the exarch protoxylem strands, and the grooves were filled by the now badly shrunken thin-walled phloem and pericycle. On such specimens, prepared from regions where the stolon branches, the successive bifurcations of the protoxylem strands can be traced with ease.



Text-fig. 1. Nephrolepis volubilis. Photograph (much reduced) of portion of primary stolon \dot{p} (loosely twining) bearing several lateral plants (x). Repeatedly coiled stolons are seen at the points of origin of the lateral plants. At y, a young stolon which has not yet grasped a support.

Phlobaphene is commonly found in ferns, impregnating the walls of ground tissue cells just outside the endodermis, and is well-known for its great resistance to acids.\(^1\) Of a piece of the stolon about half a centimetre long kept in concentrated chromic acid for some days, all parts had been destroyed except the phlobaphene in the inner cortical layers, which was left intact as a black hollow cylinder. This method may perhaps be of use in following the intricate vascular structure of certain other ferns, in which the phlobaphene-containing layers closely invest the vascular strands.



Text-fig. 2. N. volubilis. Natural size photograph showing three lateral plants. The cut ends of the primary stolon show the single axial strand. Scabs cover the secondary stolons and the lateral plants.

III. DESCRIPTION OF NEPHROLEPIS VOLUBILIS J.SM.

(a.) External Features and Distribution. This species, which ranges in distribution from Northern India, through the Malayan Region to New Guinea, is distinguished chiefly by its peculiar habit. The main axis gives rise laterally to stolons of unusual length which, instead of creeping about on the substratum as in the other species of the genus, scale forest trees up to a height of 16 metres and thus raise the young plants, produced on them at intervals, far above the level of the ground vegetation of which the mother-plant forms a

Walter, Bibliotheca botanica, iv, p. 15, 1890.

² Christ, l.c.

part. The particular specimen that Mr. Brooks saw was at least 10 metres in height and was scrambling over bushes on to a tree at the outskirts of a forest.

The stolons are stiff, cylindrical organs, devoid of ramental scales in the older parts; the surface is smooth, except for the scars of fallen branches (Text-fig. 2), or for occasional dormant buds.1 Faint brown spots mark the positions of lenticel-like structures, while the minute scars of fallen ramental scales are also distinguish-Short branches, which may be called secondary stolons, come off at frequent intervals almost at right angles to the primary stolon, and differ from the latter in being covered with scales (Text-fig. 2).2 Distally each secondary stolon bends rather sharply upwards, and is continued into the short axis of the daughter-plant,3 which carries a tuft of 2-4 leaves in addition to a similar number of thin, wiry, unbranched stolons. The striking appearance of these stolons is well illustrated by the photograph where they are seen coiling repeatedly round adjoining petioles; they apparently serve as efficient climbing organs. In the young condition they are neither coiled, nor so stiff, as they become after having grasped a support.

In the material available none of the daughter plants showed any trace of roots, nor were there any roots on the stolons. This circumstance is easily understood so long as the daughter-plants are attached to the stolons which connect them with the absorbing system of the mother-plant.

(b.) Anatomy. In transverse section, the stolon bears a very close resemblance to the rhizome of Lygodium.

The Primary Stolon⁴ is about 2.5 mm. in diameter, of which about 1 mm. is formed by the xylem-cylinder in the form of a fluted column composed of tracheids and parenchyma. In transverse sections (see Pl. IV, figs. 1 and 2) the parenchyma appears as tortuous 1-3-seriate chains of thin-walled cells with normal contents. In longitudinal section, these cells appear in vertical rows and are

¹ Sperlich, Flora, 1906, p. 463, pl. iv, fig. 2 (N. cordifolia).

² At this stage it should be made clear that there is no marked line between the "lateral plant" and the "secondary stolon." In fact, it may even seem advantageous to leave out the term secondary stolon, and consider the lateral plant as arising directly on what we have termed the primary stolon.

² One case was observed where it was continued into a short piece which was identical in character with the primary stolon, the latter becoming arrested. This piece again produced a branch exactly like a primary stolon, and itself became arrested.

⁴ Already described for *N. exaltata* by Lachmann ("Contributions à l'histoire naturelle de la racine des Fougères," Lyon, 1889) and by Chandler (Ann. of Bot., 1905, p. 392) and Sperlich (l.c., p. 464 ff.) for *N. cordifolia*.

several times longer than broad, with horizontal or oblique end-walls, probably forming a connected system. The cells store abundant oval starch-grains in the mature parts of the stolon. The metaxylem elements are all finely scalariform and develop centripetally, the larger tracheids being nearer the centre. The protoxylem consists of narrow annular and spiral tracheids grouped in 7-9 distinct exarch strands forming the ridges on the xylem-cylinder. Each protoxylem strand is traversed by one or two longitudinal rows of parenchyma cells.

The phloem is continuous round the xylem, and the proto- and meta-phloems are easily distinguishable on account of the much larger elements of the latter. Taking the metaphloem first, the sieve-tubes occur in distinct crescentic groups occupying the bays between the protoxylem ridges, and separated from the latter and from the metaxylem by one or two layers of parenchyma. The largest sieve-tubes of each group occur in the middle of each bay. Their walls are thin and give the cellulose reaction with chlor-zinciodine; the contents are scanty and often closely applied to the walls in a thin layer containing the usual refringent granules, which become yellow with this reagent. The granules were sometimes seen filling the whole cavity of the sieve-tubes, but were often aggregated against the walls in groups which seem to mark thin places, though neither callus nor sieve-pores were visible. The phloem-parenchymatous cells are few in number and, in sharp contrast to the sieve-tubes, are full of cytoplasm and possess large deep-staining nuclei. The protophloem lies immediately outside the metaphloem, forming a well-defined layer of narrow cells about 2-4 deep. It closely follows the contour of the metaphloem, passing over the protoxylem ridges as a continuous wavy mantle (well seen in Pl. IV, fig. 1). But for this continuity round the protoxylems the the structure of the stolon would be remarkably root-like.1

The shallow bays in the protophloem are filled up by the thinwalled *pericycle*, which is 4-5 cells thick at the bays, but only two cells at the ridges so that its outer limit is circular.

The endodermis is a single layer of tabular cells with their radial walls approximately in seriation with those of the outermost pericycle layer. These walls are not thickened but stain yellow with chlor-zinc-iodine. In older parts of the stolon all the endoder-

¹ So long as this continuity exists no doubt can be entertained regarding the cauline nature of the stolon. In this relation, Heinricher's simple experiments (Flora, 1907, pp. 57, 63, 72) are valuable as being in the nature of demonstrations. See p. 266 below.

mal walls give this reaction. Some of the endodermis cells were found to be traversed in the radial direction by peculiar struts (Pl. IV, fig. 2) loosely attached by their flat ends to the respective tangential walls, and often becoming free by one or both ends. In unstained preparations, these objects appear homogeneously yellow and translucent. They stain bright red in gossipimine or safranin but remain unaltered in chlor-zinc-iodine. Their significance is obscure but they may serve a mechanical function similar to that ascribed by Schwendener to the so-called Casparian strips on the radial endodermal walls of many plants.

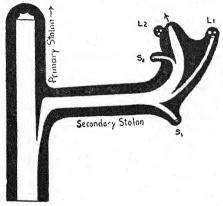
The cortex falls into two well-marked zones. The inner consists of about a dozen layers of cells. The walls of the layer immediately in contact with the endodermis are extremely thick, perforated by deep, straight pits, and thickly impregnated with phlobaphene. Eau de Javelle quickly bleached this substance; the lamination of the walls became evident, and a violet colour with chlor-zinc-iodine showed the presence of cellulose. The remaining cells of the inner cortex are large, and rounded or oval in cross-section, with abundant triangular inter-spaces. In the younger parts of the stolon, these cells have thin walls, numerous chloroplasts and large oval starch-grains. As the stolon becomes older the walls become thickened and pitted, and to some extent impregnated with phlobaphene, while the contents gradually disappear, the tissue assuming a purely mechanical function.

The outer zone of the cortex consists of about ten layers of rather narrow cells with lignified³ walls, closely packed without inter-spaces. In regions corresponding to overlying stomata, however, the cells of this otherwise air-tight sheath are thin-walled and loosely packed as in the lenticels of higher plants, and the sub-stomatal chamber is thus brought into communication with the air-system of the inner cortex. These channels persist long after the death of the stomata.

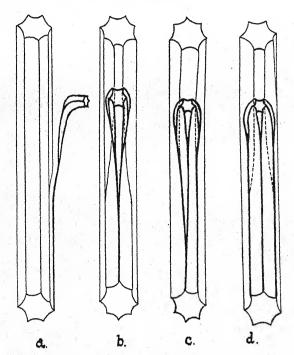
- 2. The Secondary Stolon is, in the main features of its anatomy, very similar to the primary stolon, but has a thinner xylem-core and relatively wide cortex, which is uniformly thick-walled, except for its one or two innermost layers which are left thin-walled. The air-space system is much reduced. In the endodermis, the "struts" (see above) are much shorter. The pericycle
 - ' Haberlandt, "Physiological Anatomy," p. 371, Engl. Transl., 1914,
 - ² Sperlich states that these walls are suberized in N. cordifolia (1.c., p. 467).

³ This was confirmed by Wiesner's phloroglucin and hydrochloric acid test, as well as by ammoniated fuchsin.





Text-fig. 3. N. volubilis. Diagrammatic longitudinal section through the lateral plant and the region of branching of the primary stolon. S_1 S_2 , two stolons arising on the lateral plant. L_1 L_2 , leaves, each possessing three strands. Cortex black, vascular strands white.



Text-fig. 4. N. volubilis. Diagrams to illustrate behaviour of protoxylems in region of branching of primary stolon. The vertical fluted column is the xylem-cylinder of the primary stolon, the ridges being the protoxylem strands. The protoxylems supplying the secondary stolon are represented in bolder lines. The broken lines in b, c, d, represent the portions of strands passing behind the secondary stolon. a is a side view of b. For further explanation see text.

is practically uniform in thickness all round. In the sieve-tubes the refringent granules are more numerous and the protoxylem groups often fewer by one or two than in the primary stolon.

The mode of origin of the secondary stolon is illustrated by the diagram in Text-fig. 3. The branch strand is thin to start with, and runs for a couple of millimetres nearly parallel to the vascular cylinder of the primary stolon and still enclosed in the cortex of the latter, at the same time gradually widening out. Then it sharply turns away almost at right-angles to its previous course, forming a a striking knee-like bend. Attention may here be called to the resemblance of this mode of branching to the origin of the so-called "axillary branches" in the Hymenophyllaceæ and the Botryopterideæ. A comparison of Text-fig. 3 with Boodle's figure of a longitudinal section through the region of branching in Trichomanes radicans is interesting, even if it only brings out a superficial resemblance.

At the actual point of branching, forked or V-shaped tracheids (all scalariform) were seen, similar to those observed by Boodle³ in Lygodium. The tracheids in the ascending part of the branch-strand are very short and more or less distorted.

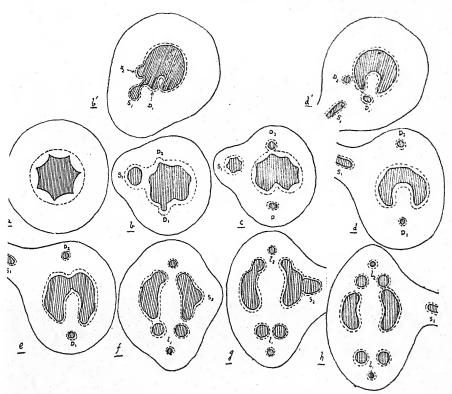
The behaviour of the protoxylem strands is interesting. Text-fig. 4 shows diagrams drawn from steles actually dissected out, and based on several specimens which could be reduced to the three types, b, c, d. In this figure, a represents a side-view of b. The preparation for the branching of the stolon is often apparent as much as half-a-centimetre below the point where the stele forks. One, two or three of the protoxylem-strands of the primary stolon, which are destined to supply the secondary stolon, pass upwards and divide as shown (thicker lines) the branches gradually spreading round the metaxylem cylinder of the secondary stolon to the extent that the latter becomes free from the main. The median protoxylem is entirely given over to the branch-supply, but each supplementary one, when present, partly supplies the branch, and is partly continued into the main. The number of protoxylem-groups in the main stolon, above and below the point of branching remains

¹ Though Sperlich (l.c., p. 462) goes into the branching of the stolons in N. cordifolia, the relations of the vascular structures have not been elucidated.

² Boodle, Ann. of Bot., 1900, fig. 28, pl. xxvii.

³ Boodle, Ann. of Bot., 1901, pp. 367-8. In one preparation of *N. rufsscens* var. Whitmanni two or three V-shaped tracheids were seen fitted together in a row, while in another one two curved sieve-tubes were observed similarly arranged.

more or less constant: the diagrams illustrate the different ways in which this object is attained.



Jiez Text-fig. 5. N. volubilis. Serial sections through basal part of lateral plant. a-h are from one plant, b' and d' from another to show the varying relative positions of the stolon- and leaf-strands. S_1 S_2 , first and second stolons; D_1 D_2 , dorsal strands of first and second leaves, respectively. Xylem shaded, endodermis shown as a broken line.

3. The internal structure of the Lateral Plants in Nephrolepis, except for Trécul's¹ short account of his unnamed plant, remains undescribed. A comparison of the lateral plant in N. cordifolia with Chandler's² description of the "sporeling" of that species revealed certain differences which will be noted below (p. 263). It is unfortunate that for N. volubilis such a comparison is impossible till plants raised from spores are available, but a description of the lateral plant may be given.

¹ Trécul, l.c. p. 245.

² Chandler, l.c. p. 389.

The changes that occur at the base of the lateral plant are shown in Text-fig. 5. They comprise the origin of two stolons (s₁, s_2) and two leaves (l_1, l_2) . The stolon bundles never leave gaps. Concurrently with the origin of the first stolon, two small strands are separated off from the central cylinder, one on each side of the stolon (D_1, D_2) ; these form the dorsal strands of the two compound leaf-traces, there being no simple traces in the lateral plant. The solid central cylinder rapidly becomes horse-shoe shaped, (c, d, d^{1}) by an invagination of the cortex, which pushes the endodermis, pericycle and phloem before it. The dorsal strand of the first leaf (D_1) turns round so as to lie opposite the invagination. This small strand is clearly not responsible for the relatively huge gap which it subtends and which rapidly deepens, giving the cauline strand a distinctly horse-shoe like form as seen in section (d). In fact the dorsal strand does not contribute at all to the formation of the invagination. The latter presently breaks through to the opposite side of the horse-shoe, dividing it into two large curved strands (e, f). It is clear that this stage cannot be called a dictyostele, for the gaps are not leaf-gaps. From the ends of the large strands opposite D_1 , two relatively large ventro-lateral strands are constricted off, and these three together form the first leaf-trace (l_1) which is compound.

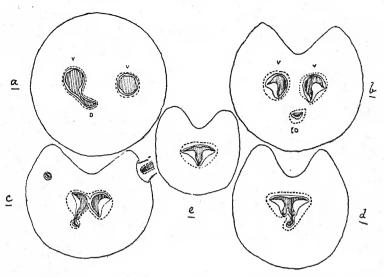
It may be pointed out that by the separation of the two ventrolateral strands, the gap, from whose sides they come off, becomes larger, and the first leaf-trace may, in a sense, be said to be responsible for a portion of the gap, though not for its initiation.

A second stolon (s_2) arises exactly like the first and at the same time the second leaf-trace (l_2) is completed, exactly like the first.

Before the first gap (that opposite the first leaf-trace) is closed up, the dorsal strand of the third leaf arises at a different point on the cauline stele, causing a distinct gap, and being followed at a higher level by its two ventro-laterals. A fourth leaf may soon arise similarly, so that the vascular structure at the apex of the lateral plant is a primitive form of dictyostele.

Beyond a rough numerical correspondence there is not much to suggest any relation between the stolon and the leaves. The origin of a stolon is frequently, but not always (as shown by b^i , d^i in Text-fig. 5) along a radius at right-angles to the one on which the nearest leaf is situated.

The stolons borne by the lateral plant, which may become tendril-like, are similar to the secondary stolons in internal structure.



Text-fig. 6. N. volubilis. a-e Serial sections through leaf from base towards apex. a is at the extreme base, e very near the apex. Xylem shaded, protoxylem solid black, phloem within the continuous line, endodermis, a broken line.

The petiolar structure was described for Nephrolepis in general terms by Trécul1 long ago, though no figures were given. These may now be given for N. volubilis (Pl. 4, fig. 3; Text-fig. 6). Immediately before the three leaf-trace strands enter the petiole, the dorsal anastomoses with one of the vento-laterals (a) but it soon becomes free again. The petiole at this stage is circular in section. The usual adaxial groove soon appears on it, and at the same time the outline of the xylem portion of each strand, nearly circular at first, becomes crescentic in the manner shown (b) the positions of the protoxylems being indicated in solid black, while the metaxylem is shaded. Phloem completely surrounds the xylem, being particularly abundant in the deep bays at the outer side of each ventro-lateral strand. The strands to the pinnæ are given off from the adaxial horn of each crescent (c). The dorsal strand, passing up through the long rachis, anastomoses alternately with the two ventro-laterals twice or thrice with each. Ultimately, however, it loses itself into one of them (d-e). Meanwhile, the latter approach each other (c) by their convex sides and fuse along the middle-line, forming the T already mentioned by Trécul (e).

The stage e deserves notice on account of its similarity to a transverse section of the petiole of Lygodium japonicum. As in that

¹ Trécul, Ann. Sci. Nat. V, t. 10, 1869, pp. 351-2.

plant, the parenchymatous xylem has "three prominences, one median and two lateral, where the first formed tracheids occur," while between these are bays where the phloem is thickest. It is interesting to find near the tip of the leaf of a Polypodiaceous fern a stage recalling the primitive condition of Lygodium. The almost identical plan of structure, as seen in a transverse section, of a Lygodium stem and the stolon of Nephrolepis volubilis has already been referred to (p. 254).

Nephrolepis leaves are well-known to bear chalk-glands on the upper surface of the pinnæ. These have been described by Poirault' in species of Polypodium, and very similar ones were found in N. volubilis. The photograph (Fig. 4) on Pl. 4 is intended to show the "spoon" shape in vertical longitudinal section, mentioned by Poirault. The large, round or oval black bodies are apparently resinous, but some of them are the prominently staining large nuclei of the parenchymatous cells between the swollen reticulate tracheids. A couple of spiral and annular tracheids are seen in the vein coming up to the gland.

IV. OTHER SPECIES OF THE GENUS.

Having reviewed the anatomy of N. volubilis we may pass on to the consideration of a few of the other species which were examined.

(1) N. cordifolia. Sperlich's excellent account of the stolons of this plant leaves little to be said. From the base of the numerous roots on the stolon a longitudinal groove extends towards the apex of the stolon, sometimes for a considerable distance, so that a cross-section through this region is not quite circular. Each groove always overlies one of the four protoxylem strands of the stolon, the roots arising in four orthostichies.

The mode of branching of the primary stolon shows no important difference from that in N. volubilis. On account of the small size of the stele, it is not possible to dissect it out neatly enough to show the behaviour of the protoxylem strands in the secondary stolon, though it is clear that one of the four protoxylems of the primary stolon is continued into the secondary, while serial transverse sections in the region of branching lead to the belief that the further branching of this strand is on the same general plan as in N. volubilis.

¹ Boodle, l.c., p. 366, fig. 4, pl. xix.

² Poirault, Ann. Sci. Nat. VII, t. 18, p. 250 ff.

^{*} Sperlich, I.c., p. 464.

A study of the lateral plant revealed certain interesting differences from Chandler's account of the sporeling. The most striking feature in which the lateral plant differs is the comparative rapidity of its development. This difference may perhaps be explained by the fact that the two kinds of plants start life at different stages, the lateral plant having a better start than the sporeling, on account of the ready-made channels of food- and water-supply afforded by the well-developed stolon at its base. This comparative rapidity of development finds expression in the fact that the first leaf may be well-developed and possesses a compound leaf-trace, whereas in the sporeling it is not till after the fourth leaf that such a condition is reached. The primitive stage of the simple arc-like trace described by Chandler on p. 391 is also thus skipped over by the lateral plant.

- (2) N. Whitmanni. I am indebted to Mr. Lynch for kindly ascertaining that this is a garden variety of N. rufescens Presl. Material of the stolons and of lateral plants obtained from the Cambridge Botanic Garden, showed such a close correspondence in external and internal structure and in the mode of branching, even in details, with N. cordifolia, that no more need be said about it. The stolons in one specimen had attained a length of nearly two metres, and were still growing vigorously.
- (3) N. rufescens tripinnatifida.³ In the usual structure of the stolons this plant is identical with the above, and is only mentioned here because one case of branching was seen (? abnormal) which looked exactly like that mentioned by Lachmann⁴ for N. Duffii. Transverse sections showed that the preparation for the division of the axial strand began at a distance of not less than three centimetres from the actual fork. A root arose in the neighbourhood of the fork, but not exactly at that level; its bundle ran for about 2-3 mm. inside the cortex of the stolon before entering it.
- (4) N.Duffii (according to Goebel⁵ a mutation from N. cordifolia). A photograph is given (Pl. IV, fig. 5) of a cross-section of the forking stolon in order to show the relation of the four protoxylem groups of each arm with one another and with the root-strand. The latter has apparently been given off by the stolon on the right-hand side,

¹ Chandler, l.c., p. 389.

² Chandler, I.c., p. 391.

³ According to Baker (Ann. of Bot., 1891, vol. V, p. 331) a garden form of N. acuta Presl., itself closely allied to N. rufescens Presl.

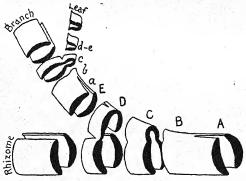
⁴ Lachmann, I.c., pp. 149-50., Pl. V, figs. 17-20.

⁵ Goebel, Flora, 1907, p. 42.

whose protoxylems show evident sign of derangement, the one opposite the root-strand having become reduced in size.

It must be pointed out that it is by no means general for a root to appear at the level of the bifurcation. On the other hand, several may be present at or near the point. It is true a case where a root arises at the bifurcation is strongly suggestive of a rhizophore arising at a bifurcation of the stem in Sellaginella, as Lachmann points out.

(5) N. ramosa Moore. Herbarium material only was available of this species and of N. altescandens. No stolons are borne, but the rhizome itself is slender and creeps on the trunks of trees. The rhizome frequently gives off side-branches which bear distant leaves in two rows, alternately right and left, like the main rhizome itself. The branch has an internal structure, and leaf-arrangement, identical with that of the main axis, so that only the internodal structure and the mode of origin of the branch and the leaf need be described (see Text-fig. 7 and Pl. IV, fig. 6).



Text-fig. 7. N. ramosa Moore. Diagram of vascular skeleton to show the origin of a branch-trace from the rhizome, and of a leaf-trace from the branch. In the natural position the two meristeles of the stem are dorsal and ventral, with the gaps right and left. The cut ends of the strands are shown black. A-E, stages in the origin of the branch trace; a-e, corresponding stages in the origin of the leaf-trace. Note the great similarity in the corresponding stages. At d-e the leaf-trace is almost divided into two strands.

The vascular cylinder at the internode consists of two curved strands facing each other (Text-fig. 7, A), but separated from each other, and surrounded by a thick layer of sclerenchyma (black in the photograph on Pl. IV, fig. 6). Each of the strands has its own phloem, pericycle and endodermis, and they lie in the dorso-ventral plane, the gaps between them being thus respectively on the right and left. These gaps are very long, for they overlap in spite of the fact that the leaves are more than 2.5 cm. distant on the thin wiry rhizome.

In preparation for the origin of a branch, the gap on the side on which the branch is to arise is closed by the bundles approaching each other and finally fusing (B) by their margins. The portion of the xylem where this fusion occurs, at the same time bulges out sideways as an arc (C) seen in section, to the formation of which the two strands have contributed equally. This arc is the branch-trace. It soon frees itself first from one (D) and then from the other cauline strand, and at this stage passes out as a C-shaped strand into the branch, with its gap facing the main rhizome. Very soon, however, its opposite side opens, and the internodal structure of the main axis is thus established in the branch (E).

The mode of origin of the leaf-trace is almost identical with that of the branch, and need not be described fully. On entering the petiole the C, which is formed exactly like the branch-trace, but is smaller, becomes very much attenuated on its abaxial side, and may even split into two strands corresponding to the two internodal strands. This division, however, is only momentary, and the leaf-trace very soon assumes the form shown in Pl. IV, fig. 8,2 its adaxial margins turning outwards and becoming engaged in supplying the pinnæ. In addition to peltate scales (s) the sides of the rachis bear curious stiff, mostly unicellular hairs (h).

(6) N. altescandens (Colla) Baker. This species from Juan Fernandez, is closely related to the above, and the agreement extends to anatomical characters. The internode has exactly the same structure as in that species. The origin of the leaf-trace is different; each internodal strand constricts off a small strand which forms half of the leaf-trace (Fig. 7, Pl. IV) which thus at its origin consists of two separate small strands instead of a single large one. The two leaf-strands on entering the petiole join each other and the resulting strand assumes the form shown in Fig. 8, Pl. IV.

The origin of the branch is exactly the same as in *N. ramosa*. Fig. 7, Pl. IV shows a section which happens to have passed through a point where a leaf and a branch were both being given off from the rhizome, diametrically opposite to each other. (Such a case was met with only once, the usual course being for the leaves and the branches to come off from the rhizome at consider-

¹ In one specimen from the Kew Herbarium (Pl. IV, fig. 6) the tracheids near the middle of one of the internodal strands were either very narrow or absent, forming a break in the xylem, though the phloem passed round the bundle in the normal way. This interruption was not seen in a specimen from the Cambridge Herbarium.

² This figure will do equally well for N. ramosa and N. altescandens.

³ Christ, l.c., p. 288.

able distances apart). In the figure referred to, the two leafstrands are still just attached to the ends of the cauline strands on the one side, while on the other the arc-like branch-trace is constituted by the attenuated portion of the xylem-ring.¹

From the foregoing account of the species of Nephrolepis three interesting facts emerge. Firstly, an evident tendency in the genus for the products of branching of the stolon to remain adnate to one another for shorter or longer distances, so that their respective vascular strands lie more or less parallel to each other and enclosed within a common cortical envelope, before they finally become free. Secondly, the great uniformity in structure and mode of branching of the stolons in the different species, even when their habits are divergent. Thirdly, the great similarity of structure, in N. ramosa Moore, between the basal part of the leaf, and the stem on which it arises, and the exactly similar way in which the leaf- and branch-traces respectively originate. In this respect N. ramosa agrees with Trichomanes radicans and other members of the Hymeno-phyllaceæ.

It may also be mentioned here that in the two closely allied species N. ramosa and N. altescandens, we see the transition from the simple arc-like leaf-trace of the former to the more advanced double trace of the latter.

V. BIOLOGICAL OBSERVATIONS.

There is abundant literature dealing with the biological aspects of Nephrolepis centred especially on the tubers and the stolons. Three of the most recent papers, two by Sperlich,² one by Heinricher,³ contain a series of highly interesting observations on the growth and development of the tubers and stolons, studied by the latter author under artificial conditions of culture. Of these results the most remarkable appears to be Heinricher's exposition of the great plasticity of the stolons which, moreover, can be controlled by the cultivator. For instance, by merely covering the rhizome over with earth he was able to transform it into a stolon which bore leaves directly, and possessed a single axial strand.⁴

¹ It must here be stated that the above account of N. ramosa and N. altescandens is based on a limited amount of dried material.

² Sperlich, Flora, 1906, p. 451; Flora, 1908, p. 341.

³ Heinricher, Flora, 1907, p. 43.

^{4 1.}c., p. 63. See also pp. 57, 72.

It may be instructive to study the behaviour of the vascular strands at the origin of such leaves borne directly on the stolons, and to ascertain whether such a stolon agrees with the normal stolon in internal structure.

A few remarks on the stolons of some Nephrolepis plants which I had the opportunity of observing at the Cambridge Botanic Garden may now be made. The plants were all in the same house (Tropical Fern House).

- (1) N. Whitmanni.—In a wire cage hanging vertically down about 8 feet from the ground. The primary stolons, $1\frac{1}{2}$ -2 feet long, were all seen growing directly downwards. They bore no roots, unlike the stolons of all the specimens that were not in hanging pots; and were less frequently branched than usual.
- (2) N. Whitmanni, N. davallioides (Sw.) Kze., and N. todeaoides.\(^1\)—One specimen of each in a pot placed on a table covered with moist pebbles. In each case most of the stolons arising from the stock on different radii, on reaching the edge of the pot, passed close over the edge and then grew obliquely outwards and downwards towards the table at an average angle of about 45° to the table, the tips in each case being above the level of the table.\(^2\) They bore secondary stolons usually only on their lower sides, and these grew vertically downwards, never, however, touching the table.
- (3) N. cordifolia.—A large specimen bore over 35 stolons, 34 of which, after passing over the edge of the pot, grew vertically downwards, the single exception growing obliquely outwards and downwards at about 45°. Several of the vertical stolons, on reaching the moist table passed underneath the pot.
- (4) In an unnamed specimen growing in a pot, the stolons were mostly growing downwards but adhering to the outside of the pot.

No definite solution could be arrived at regarding the varying behaviour of the stolons in the above four cases. Number 1 might suggest positive geotropism but the stolons, especially when long, would hang down merely by their weight. Number 3 is a partly similar case, but the passing of the stolons under the pot suggests positive hydrotropism, which is also suggested by Number 4.

Although it did not appear likely that these directions of growth were due to mere chance, (because of the considerable

¹ This is probably a garden variety.

² This appearance was afterwards seen illustrated (in fig. 90, p. 477 in Gard. Chron. I, 1887) for N. rufescens var.

uniformity of behaviour of the stolons in each individual pot), some of the vertical stolons in pot 3 and some in pot 2 (N. todeaoides) were artificially propped up on wooden sticks so as to remain horizontal. After a week or ten days the bent tips of the stolons in each case showed evident signs of re-adjusting themselves to their former directions of growth; and in pot 2, some new secondary stolons which had developed during this period on portions of the primary stolon distal to the bend, grew vertically downwards as expected.

Case 2 may at first seem inexplicable, and it was the one most frequently met with, but perhaps it can be interpreted in the following way. If it were not for the proximity of the moist table on which the pot was placed, the stolons would probably tend to grow approximately in a horizontal direction, till they become too long, when their weight would come into play. The presence of the moist substratum, however, calls forth a positive hydrotropic response. The oblique position taken up by the stolons would thus be a compromise between two tendencies, the horizontal and the vertical.

No marked geotropic response seems to be exhibited by the stolons. The case of the vertically-growing stolons in the hanging plant mentioned above is probably to be explained, mainly at least, by the weight of the long stolons. Any geotropism, if present, must be weak. According to Lachmann, the stolons produced on the underground region of the principal axis are geotropically less sensitive than the roots of most ferns. Sperlich who in 1906² expressed the belief that the subterranean stolons of Nephrolepis are positively geotropic, in 1908³ withdrew this view in favour of positive hydrotropism.

In the later paper just cited (p. 356) Sperlich raises the question whether Nephrolepis stolons are also sensitive to contact stimuli. The curious way in which the stolons pass close over the edges of the pots (see p. 267) is rather suggestive, but Nephrolepis volubilis affords a case which reminds one strongly of the tendrils of higher plants (Text-figs. 1 and 2). In Text-fig. 1, a portion of the long primary stolon (p) is shown bearing several lateral plants (x), while surrounding the points of origin of these lateral plants are seen the close coils of the tendril-like stolons, two of which are

¹ Lachmann, Contributions, etc., p. 150.

² Sperlich, Flora, 1906.

³ Sperlich, Flora, 1908, p. 354.

shown (natural size) in Text-fig. 2. It will be seen that the direction of coiling does not show any regularity. When young, these stolons are comparatively soft and pliable (one such young stolon is visible in Text-fig. 1, y), but the older ones, after coiling round supports become wiry on account of the very thick-walled cortex. These structures are undoubtedly of great help in supporting the primary stolon during its growth upwards among bushes and trees. The primary stolon itself may be seen to be loosely twining in Text-fig. 1.

Attention has already been drawn on p. 253 to the extraordinary habit of N. volubilis. The primary stolon makes it possible for the lateral plants to reach a very considerable height on trees, and though these lateral plants appear to be devoid of roots it is possible that these may develop when the plants are artificially severed from the stolon on which they are borne. From the large number of scars of fallen lateral plants on the primary stolon the surmise may perhaps be ventured that the lateral plants may be shed from the stolon after they have formed their leaves at the expense of the mother-plant.

Sperlich's view regarding the origin of epiphytism in Nephrolepis is peculiarly borne out by the plant under consideration. He regards the possession of stolons by Nephrolepis as having probably been the initial stage in the gradual emancipation of the plant from the soil. This would be an analogous case to that of many phanerogamic epiphytes which according to A. F. W. Schimper have evolved from lianes rooted in the soil. The occurrence, within the genus, of a facultative epiphyte like N. cordifolia may not, perhaps, be quite without significance in this relation.

VI. THEORETICAL CONSIDERATIONS.

We may pass now to some of the considerations of theoretical interest attaching to the genus Nephrolepis. Of these, the one that has aroused the most prominent interest of investigators is undoubtedly the morphological nature of the stolons, which was responsible for the Lachmann-Trécul controversy,² the former author holding that they were cauline structures while the latter contended that they were roots. This question would seem to have

¹ Flora, 1908, pp. 357-8 and 360.

² Various papers in the Comptes Rendus, of which only the following need be mentioned: Lachmann, vol. CI, 1885, p. 603; Trécul, vol. CI, 1885, p. 920; Trécul, vol. CVIII, 1889, p. 1081. See also Lachmann, Contributions, etc., 1889.

been closed long since, till Velenovsky in 1905¹ propounded his view that the stolons of Nephrolepis belong to a new morphological category which he called "Achsenträger" (shoot-bearer). This term, as applied to these organs has been severely criticized by Sperlich, and Velenovsky has recently attempted to defend his position.² Nevertheless, there seems little room for a new morphological category for the reception of a structure whose cauline nature is decided beyond question (p. 255, footnote). It will suffice here to summarize in the form of a table the several views that have been put forward by various authors regarding the nature of the stolons.²

Root.	Shoot.	Combining Root & Shoot Characters.	An Organ sui generis.	
Brongniart 1839 Trécul 1885	Kunze 1849 Hofmeister 1857 Russow 1873 Lachmann 1885-9 Goebel 1889 Poirault 1893 Sperlich 1906, 1908 Heinricher 1907	De Bary 1887		

We have seen that the outstanding feature of the stemanatomy of the species of *Nephrolepis* examined is the presence, near the apex, of a primitive type of dictyostele (not far removed from a solenostele), while in the leaf-trace we pass from the simple arc-like condition (*N. ramosa*) to the compound (double in *N. altes*candens, triple in *N. volubilis*).

So far as anatomical characters can be a guide to phylogenetic position, Nephrolepis would seem to occupy a place in that more or less coherent but intricate plexus of forms which illustrates, on the one hand, the transition from the solenostele to the dictyostele (with concomitant elaboration of the leaf-trace), and on the other, the "phyletic shift" of the sorus from the margin of the frond to its under surface. In the latter respect Nephrolepis is evidently well advanced towards the superficial type of sorus. For the location of the genus within this plexus of forms more data from

¹ Vergleichende Morphologie der Pflanzen, 1905, vol. I, p. 233, Prag.

² l.c., vol, IV, 1913, p. 32.

³ The references up to 1888 will be found in Lachmann, Contributions, etc., of the later ones the following may be mentioned: Goebel, Pflanzenbiologische Schilderungen, vol. I, 1889, p. 203, footnote; Poirault, Ann. Sci. Nat. Bot., 7, sér. t. 18, p. 160.

the anatomy of the mother-plant are necessary than are at present available.

The foregoing sketch of the range in habit and structure exhibited by the species of Nephrolepis may perhaps justify the following view regarding their relative positions within the genus. That a well-marked tendency towards the epiphytic habit is exhibited by most of the species of the genus is abundantly clear from what has preceded. Starting from a hypothetical solenostelic form with a short erect stock bearing leaves with simple leaf-traces, the epiphytic tendency may be considered to have found expression in two ways, and to have led to the gradual evolution of two main types of habit. On the one hand, the stem itself became a scandent rhizome bearing distant leaves, and forms like N. ramosa and N. altescandens were evolved. On the other hand, a much more specialized and highly efficient organ, the stolon (which is probably to be taken as a highly modified branch of the stem) was evolved for the purpose, with conspicuously successful results (N. volubilis, N. cordifolia).

The leaf-trace, along each of these two lines of progress, followed a course of elaboration of its own, from the simple (N. ramosa) to the compound (N. altescandens), along the first of these lines. Sufficient data are not available to enable one to delineate accurately the course of elaboration through which the leaf-trace passed in the stoloniferous forms. However, there is an indication (a faint one it must be admitted) that the evolution of the leaf-trace was less gradual in this series, for in N. cordifolia the simple arc-like trace described by Chandler in one of the earlier-formed leaves of the sporeling soon gives place first to a double and then to a triple trace in the later leaves.

In this relation a detailed study of the sporelings of different species of Nephrolepis, on the lines of Chandler's work, would probably throw considerable light on the question. That a study of the lateral plants, (which are more easily obtainable) will not enlighten us to any great extent on this point is evident from the fact that, the lateral plant which, as already stated on p. 253, is produced under conditions favourable to rapid growth, no longer exhibits the earlier stages in the evolution of the leaf-trace.

If the conjecture put forward on the page just referred to has any justification, we have before us a remarkable case where exceptionally favourable physiological conditions are potent to the

¹ Chandler, I.c., p. 391

extent of eliminating from the ontogeny of a plant morphological features which probably marked important stages in its phylogenetic history.

From a study of the anatomy of N. ramosa we concluded on p. 266 that, in respect of the great similarity of structure respectively in the rhizome, branch, and the leaf at its origin, that plant formed a rather striking parallel to the case of the Hymenophyllaceæ. Although N. ramosa belongs to a phyletically much higher group of ferns, the above-mentioned feature in its anatomy may possibly go in support of the view, so strikingly borne out by the vascular structure in the Hymenophyllaceæ, that the strands of the stem and of the leaf are primitively identical structures.

Finally, the extensive development of protostelic structure exhibited by the stolons of *Nephrolepis* cannot pass unnoticed. The main axis of the plant has acquired extraordinary powers of branching, and into its branches a large portion of its energies is diverted. It seems unreasonable to regard the stolon, possessing as it does such a primitive vascular organisation, as an indication of primitiveness of the genus. Much more likely seems the view that it is a highly specialized organ whose structure may in some way be connected with the conducting functions imposed upon it.

In conclusion, I wish to express my thanks to Mr. Brooks not only for handing me the material of N. volubilis used in this research, but also for much help throughout the progress of the work. I have also to thank Mr. Boodle for valuable suggestions, and Professor Seward and Mr. Tansley for their kind interest in this investigation. I am also much indebted to Professor Seward for revising the manuscript.

VII. SUMMARY.

Nephrolepis volubilis, J.Sm., a highly specialized member of the genus, is described. The stolons arising directly on the mother-plant (primary stolons) are smooth cylindrical organs (natural size photograph, Text-fig. 2) which scale forest trees up to 16 metres and enable lateral plants, borne on them at intervals, to reach heights far above the mother-plant which is rooted in the soil.

Two to four shorter stolons which are wiry and irregularly coiled appear on each lateral plant, and seem to be contact-sensitive. They are climbing organs.

¹ Tansley, New Phytologist, 1907, p. 115.

The stolons possess a single axial polyarch exarch protostele. Where a stolon branches the two steles run parallel to each other for some distance, enclosed in the same cortical envelope, before they become free. This "adnate tendency" is also shown by the stolons of several other species examined. The structure of the stolons is remarkably uniform in the different species.

In the endodermis of *N. volubilis* (stolon) peculiar strut-like bodies were found traversing the cells in the radial direction (Pl. 1V, fig. 2). These may serve a mechanical function.

In the lateral plants the basal protostele becomes soon modified into a primitive form of dictyostele at the apex. The first leaf has a compound leaf-trace.

There are no roots on the lateral plants, but it may be that after the lateral plants have formed their leaves at the expense of the mother-plant, they are shed, and strike root on the ground. This is suggested by numerous scars on the primary stolon.

The primary stolons of several species of *Nephrolepis* (p. 268) are probably positively hydrotropic.

In N. ramosa and N. altescandens, two closely allied species without stolons but with scandent rhizomes the internode possesses the simplest type of dictyostele imaginable (viz., two strands separated by two leaf-gaps as seen in cross-section). In N. ramosa the vascular structure at the base of the branch and leaf-traces is almost identical, and recalls the condition in the Hymenophyllaceæ, which has been previously used in support of the view that stem-stele and leaf-strand are primitively identical structures.

In N. altescandens the leaf-trace arises as two separate strands, in N. ramosa as a simple C-shaped strand.

Sperlich's view regarding the origin of epiphytism in the genus (p. 269) is well borne out by a study of N, volubilis. He regards the appearance of the stolon as having been the initial stage in the gradual emancipation of the plant from the soil.

Velenovsky's adoption of a new morphological category, the "Achsenträger" (shoot-bearer), to include the stolons of Nephrolepis, has no justification in view of the evident cauline nature of these organs.

The primitive organisation of the stolon is not indicative of primitiveness of the genus. More probably it is an organ highly specialized for the conducting functions entrusted to it.

Possibly because of the exceptionally favourable physiological conditions in which it is placed (connected by the stolon to the

absorbing system of the mother-plant) the lateral plant of $N.\ cordifolia$ (and perhaps of other species) in its ontogeny omits some of the earlier stages in stelar evolution which are shown by the sporeling (see pp. 260 and 263).

THE BOTANY SCHOOL, CAMBRIDGE,

September, 1915.

EXPLANATION OF PLATE IV.

ILLUSTRATING MR. SAHNI'S PAPER ON THE ANATOMY OF NEPHROLEPIS,

(The figures are all from photographs).

- 1. N. volubilis. Transverse section of mature primary stolon, showing on the left the strand of a secondary stolon. Small-celled lignified outer cortex. Innermost cortical walls extremely thick, containing phlobaphene, seen as a black ring round the stele. Protophloem, a continuous wavy layer passing round the eight protoxylems. Phloem filling the bays in the xylem-cylinder, and separated from the tracheides by parenchyma. x abt. 24.
- 2. N. volubilis. Part of transverse section of young primary stolon. Thinwalled inner cortex with triangular inter-spaces. The phlobaphene-containing walls comparatively thin. In three of the endodermal cells the "struts" (p. 256) are seen, two having become free by their inner ends. s, sieve-tubes; t, metaxylem tracheides which are yet thin-walled, only the protoxylem elements being lignified. \times abt. 130.
- 3. N. volubilis. Transverse section of petiole. Small dorsal strand and larger ventro-laterals. In all the xylem is crescentic, with phloem in the bays. Cortex as in Fig. 1. \times 50.
- 4. N. volubilis. Vertical longitudinal section of chalk-gland, showing the "spoon" shape. Regularly arranged epidermal cells in saucer-shaped depression. The gland is made up of swollen reticulate tracheides with parenchymatous cells between. The large black bodies may be resinous, but some of them are nuclei.
- 5. N. Duffii. Transverse section of forking stolon, with a root-strand above the strands of the arms of the fork. Each of the latter has four protoxylems with phloem in the bays. The root-strand has been given off from the strand on the right one of whose protoxylems is stunted. \times abt. 45.
- 6. N. ramosa (dried material from Kew Herbarium). Transverse section of rhizome showing two meristeles in dorso-ventral plane, with leaf-gaps, one of which is subtended by the arc-like trace. Sclerenchyma (black) surrounds each meristele, one of which has its xylem interrupted (see p. 265, footnote). \times 45.
- 7. N. altescandens (dried material from Kew Herbarium) Transverse section of rhizome at a point where a leaf-trace (left) and a branch-trace (right) happen to arise at the same time. Leaf-trace consists of two separate strands constricted off from cauline meristeles. The attenuated portion of the xylem on the right will pass out as the C-shaped branch-trace. × 40.
- 8. N. altescandens. Transverse section of rachis, showing arc-like strand with its adaxial ends turned outwards. On the right is a pinna-trace. s, a peltate ramental scale; h, hairs. \times 40.

THE INTER-RELATIONSHIPS OF PROTISTA AND PRIMITIVE FUNGI.

By F. CAVERS.

(Continued from p. 227).

The genus Labyrinthula includes two marine species (L. vitellina, a yellow form, and L. macrocystis. colourless, both discovered by Cienkowski in 1867) and a freshwater species (L. cienkowskii, very similar to L. macrocystis, discovered by Zopf in 1892); all three are parasitic on alge. In the active phase the organism consists of uninucleate protoplasmic units joined into a network by sparingly branched and anastomosing pseudopodia, so that it presents a striking but purely superficial resemblance to Chlamydomyxa. On encystment, which occurs as a result of drought, the amœboid units become closely aggregated and each secretes a cyst wall, while in L. macrocystis a firm common envelope is then formed in which the encysted units are enclosed. In L. cienkowskii the contents emerge from the cyst as a single mass, but in the other two species the contents divide into four within the cyst, in all cases becoming amœboid and undergoing division by binary fission so as to increase the number of units in the colony, though according to Zopf the amœbulæ on leaving the cysts may become joined up by their pseudopodia. Zopf distinguished the colony of Labyrinthula as a "thread-plasmodium," and regarded it as intermediate between the "pseudoplasmodium" of the Acrasieæ (see below, amœbulæ apposed but maintaining their distinctness) and the true plasmodium of the Myxomycetes proper (complete fusion between the uniting amœbulæ), but (especially as Zopf only inferred fusion between the amæbulæ from observing on one occasion in L. cienkowskii three empty cysts with three units in their neighbourhood) there does not appear to be much point in this suggestion. The Labyrinthula colony may equally well be compared with that seen in primitive Foraminifera like Mikrogromia, near which, in the absence of further details of its life cycle, the genus may perhaps be provisionally placed.

The affinities of the Sporozoa may be briefly considered here, for there seems little doubt that this group has, in part, arisen from the Proteomyxa along the same line as that which has given rise to the "primitive fungi" with which we are now more directly concerned. As already mentioned, the Sporozoa were divided by Metschnikoff into Ectospora and Endospora, and recent work on the group has shown that these two divisions are probably not related phylogenetically but are of quite different origin; that is, the group is an artificial one and includes two independent series of parasitic Protozoa, the general resemblances between them being due to convergence brought about by their specialised mode of life. That the Ectospora (Gregarinida, Coccidia, Hæmosporidia) are derived from Flagellata is indicated by the actual ontogenetic connexion known to exist between certain Hæmoflagellates and certain Hæmosporidia; the possession by many Coccidia of biflagellate microgametes resembling in structure the heteromastigine Plagellates; the possession by various typical Plagellates (e.g., Herpetomonas) of an attached resting-phase when the parasites become gregariniform, strongly suggesting the attached juvenile phase of many Gregarinida; the gregarinoid or euglenoid movements of Gregarinida and of the spores or other phases of Coccidia and Hæmosporidia, which are quite comparable with the contractile and metabolic movements of Flagellates; and the exogenous type of reproduction, which is easily derived from the multiple fission of certain Hæmoflagellates, and this in turn from the typical binary longitudinal fission of Flagellata in general. On the other hand, the Endospora have probably arisen from the Rhizopoda or, perhaps more probably, from those members of the Azoosporeæ division of Proteomyxa which appear to lead to the Rhizopoda and other Sarcodina. A Flagellate ancestry is apparently excluded by the entire absence of a flagellate or even gregariniform phase and by the simple type of spore formation characteristic of the primitive Endospora. Some of the latter. belonging to the group Haplosporidia, are apparently very closely related to Proteomyxa. In some cases (e.g., Bertramia) the individual begins life as a small uninucleate body which later becomes multinucleate, then the protoplasm becomes segregated around the nuclei so as to produce a mulberry-like form, and the uninucleate spores thus formed are set free by the breaking-up of the parent body. In other cases the sporulating parasite becomes rounded off and forms a protective cyst; in others the spore mother-cells, instead of producing a single spore, give rise to several, e.g., four in Haplosporidium, many in Rhinosporidium. In Scheviakovella the amœboid individuals become aggregated to form plasmodia, and the spores divide by binary fission. Some of these simpler types of Sporozoa show striking resemblances to certain of the "primitive fungi," with which we now proceed to deal.

VI.—THE CHYTRIDIALES.

On the view here adopted there may be traced from the Proteomyxa a series of lines, or possibly a single line which branched early into diverging lines, leading to a multitude of forms which may be included in four main groups-Myxomycetes, Chytridiales, Plasmodiophorales and Acrasiales. Of these groups, representing a rough though probably fairly natural division of the "primitive fungi," the two first are very much larger than the two last, and they are also marked by the invariable presence of a flagellate phase; flagella are sometimes found in the Plasmodiophorales, but not in the Acrasiales. In all four groups the vegetative body is naked and usually capable of amoeboid movement except in various Chytridiales where a cell-wall is present in the vegetative phase so that a mycelium is formed like that of the typical Eumycetes. In other respects also the Chytridiales show a far wider range in structure and development than is to be found in the other three groups, and yet the various members of this group are so closely connected that one hesitates to break it up, at any rate to the extent to which some writers have proposed to do. In any case, we shall see that the four groups are so closely related to each other that they must be considered together, and that to separate off the Chytridiales as a group derived from algal ancestors and to combine the remaining three groups as "Myxomycetes" derived from Amæba-like Protozoa, as is done by Schröter and others, is quite unjustifiable.

In Schröter's classification in Engler and Prantl (1897) the Myxomycetes (Mycetozoa) are divided into three groups—Acrasieæ, Phytomyxineæ and Myxogasteres. Lotsy (1907) slightly rearranges this scheme by adding to the Acrasieæ the small family Labyrinthuleæ (Labyrinthula and Chlamydomyxa), thus restoring Zopf's group Sorophoreæ (distinguished by having a "false" or aggregation plasmodium in which the amœbæ do not become fused together) and applying the name Myxogasteres to the two remaining groups, in which the amœbæ fuse completely in plasmodium formation. He divides the Myxogasteres into Eumyxogasteres (Myxomycetes in the narrower and more usual sense) which have, and Plasmodiophoraceæ (Phytomyxineæ) which have not, a definite fruit-body. Lotsy, like various other writers, holds that the differences between these two groups are attributable to the parasitic mode of life of the Plasmodiophoraceæ, which are regarded as derived from the Eumyxogasteres, a view recently supported by Pavillard (1910) in his invaluable critical review of the literature of vegetable protistology. However, various considerations point to the conclusion that the Plasmodiophoraceæ have more probably originated independently of the Myxomycetes proper, though being closely related to that group, and that both are related to the Chytridiales and to the Protozoa (especially to the Sarcodina and Sporozoa). The Acrasiales (including the Acrasieæ together with certain recently described forms which may be at least provisionally placed near them) stand somewhat apart from the Plasmodiophorales (the name adopted here to include not only the Plasmodiophoraceæ but also some forms apparently best placed near this family), Myxomycetes and Chytridiales in not showing a flagellate phase and in the different type of vegetative body, but in any case the origin of the Acrasiales is doubtless to be sought in the Proteomyxa, not far from that of the other three groups of "primitive fungi."

Since, as we shall see later, there is much to be said for the view that the so-called "algal fungi" (Phycomycetes) are far more probably derived from the Chytridiales than from the green algæ, it would appear reasonable to extend the name Archimycetes, sometimes used as a synonym for Chytridiales, to include the whole of the lower fungi, which would then fall into the six divisions Chytridiales, Myxomycetes, Plasmodiophorales, Acrasiales, Zygomy-

cetes and Oomycetes. Beginning with the Chytridiales, we take as a basis for our discussion of this group Schröter's account in Engler and Prantl, as no compilation of equal scope has appeared since this was published, though in the intervening twenty years a very large amount of work has been done on these organisms. Schröter placed the Chytridineæ, together with the Ancylistineæ, in a division of the Oomycetes characterised by having the mycelium absent or feebly developed, as compared with the well-developed mycelium of the remaining Phycomycetes. In Chytridineæ the fructification is said to consist of a solitary sporangium or of a sorus formed by division, while in Ancylistineæ the fructification is divided by crosswalls into a chain of cells. The Chytridineæ are divided into six families, characterised as follows:—A. Resting sporangium formed asexually, or rarely by copulation of zoospores. a. Mycelium absent. 1. Sporangia solitary.—Olpidiaceæ. II. Sporangia aggregated in sori formed by division.—Synchytriaceæ. b. Mycelium present. I. Mycelium of delicate evanescent strands. i. Mycelium related to a single sporangium.—Rhizidiaceæ. ii. Mycelium widespread, with both intercalary and terminal sporangia.—Cladochytriaceæ. II. Mycelium of well-developed hyphæ.—Hyphochytriaceæ. B. Sexual spore formed by conjugation of contents of two sporangia

(gametangia).—Oochytriacea.

We prefer to join the Chytridineæ and Ancylistineæ as two divisions of one group, the Chytridiales. Schröter divides the Ancylistineæ into two families, the Lagenidiaceæ in which there is no definite mycelium and the whole body is divided into either sporangia or sexual cells, and the Ancylistaceæ in which a vegetative mycelium-like portion remains over after the sporangia and sexual organs have been formed. We shall now deal with the families of Chytridiales, with special reference to what appear to be the more important bearings of recent work on their inter-relationships.

In the Olpidiaceæ the fructification is intracellular and spherical or ellipsoid, rarely (Ectrogella) elongated, undivided until ripe, and produces either a thin-walled zoosporangium or a thickwalled resting sporangium. The simplest genera, like Reessia and Monochytrium, are distinguished by the actively amæboid character of the naked parasite formed by the entering zoospore. Fisch (1884) described the amorboid body of Reessia as moving about within the host-cell for a week or more by means of pseudopodia, and then giving rise to a zoosporangium the contents of which soon divided into numerous uniciliate zoogametes; these when set free united in pairs and the zygote settled upon and emptied its contents into an epidermis cell of the host (Lemna), there producing a thickwalled resting sporangium. Griggs (1910) described a new and apparently very closely related genus Monochytrium; his account is less complete so far as the life cycle is concerned, but more detailed cytologically. Here again the entering zoospores become amoboid and while some of them give rise to zoosporangia by division of the nucleus into four (meiosis?) followed after a rather extended period by repeated division of these four nuclei to form the zoospores, other amœbæ fuse together (though their nuclei remain distinct) within the host-cell and the amæboid zygote grows to form a thickwalled binucleate cyst whose further development and germination were not observed.

In the remaining genera of Olpidiaceæ (Fig. 6, A-E) the general course of the life cycle shows certain common features. The zoospores (either uniciliate or biciliate, in the latter case with one cilium directed backwards though both usually arise from the same point) have two motile stages separated by a brief period of rest, suggesting a primitive type of the biplanetism which is a marked feature of the zoospores of Saprolegniaceæ and some Peronosporaceæ—this was found by Butler (1907) and by Barrett (1912) in various species of Olpidiopsis, etc. The young parasite formed within the host-cell by the entering zoospore is at first naked and in some cases for a time more or less amœboid. In most cases there are two types of sporangium, thin-walled ones which quickly germinate and thick-walled resting sporangia, and in some cases the formation of the latter has been proved to be the result of a sexual process. In most cases the sporangia, like the naked parasite from

which it arose, lies freely within the cytoplasm of the host-cell, and the zoospores (or zoogametes, as the case may be) escape by means of a tube, or several tubes in some cases (e.g. Pleotrachelus, Fig. 6, D) which are protruded by the germinating sporangium and pierce the wall of the host-cell. In Sphærita, however, described incompletely by Dangeard (1886, 1887) the sporangium opens by decay of its wall, the zoospores being set free after death of the host Rhizopod or Plagellate: in Pleolpidium the sporangium fills the host-cell so that its membrane comes into contact with and finally fuses with the cell-wall and the zoospores escape through a pore formed by absorption of the two walls at the point of contact; and in Eurychasma, according to Loewenthal (1904) and Magnus (1905), the zoosporangium swells so as finally to burst through the wall of the host-cell, its coat opening to liberate the zoospores by means of one or more slits or pores—Petersen (1905) makes this genus the type of a new family, Eurychasmaceæ, but this appears unnecessary.

In Olpidium viciæ, Kusano (1912) observed conjugation of free-swimming zoospores (isogametes), and found that while both conjugated and unconjugated swarmers may infect the host, the former give rise to resting cysts and the latter to zoosporangia; on penetrating the host the young parasite enters the cell and comes to rest near the nucleus, being carried round by the rotation of the host cytoplasm and, though naked until nearly mature, not showing amœboid movement as in Reessia and Monochytrium. The nuclei of the zoosporangium divide during the earlier (vegetative or growth) stages by amitosis, as described by Griggs in Monochytrium, but in the later (reproductive or spore-forming) stages by mitosis. In Olpidium salicorniæ (Pig. 6, A), Nemec (1911) states that although all the naked and at first amœboid parasites appear alike, some give rise directly by repeated nuclear division to thinwalled zoosporangia, while others conjugate in pairs within the host-cell, as in Monochytrium but with fusion of nuclei as well as cytoplasm, to form zygotes which produce the resting sporangia.

Before considering some other forms which are clearly related to Olpidium and its allies, it may be noted that Schröter's family Oochytriaceæ is an unnatural one, and that the three genera constituting it (Diplophysa, Polyphagus and Urophlyctis) should be distributed among other families of Chytridiales. The genus Olpidiopsis was founded by Cornu in 1872 for a number of forms which differed from Olpidium mainly in the resting sporangium having a spiny instead of a smooth coat, and in having attached to each sporangium an empty smaller cell which he suspected was an antheridium. In 1883 Zopf described a new species, O. schenckiana, in which the sexual process was practically proved—the sexual plant arose as a single mass of protoplasm which later put out a process to form the companion cell or antheridium, this becoming completely emptied, though no actual pore was observed between it and the large remaining portion (oogonium) which developed into the resting-spore (or sporangium). Next year Fisch described a new form, Pleocystidium parasiticum, resembling O. schenckiana and like it parasitic on Spirogyra, but differing in that the sexual spores arose from two or more associated protoplasmic masses representing separate individuals; one of these became what he called the central cell (oogonium) and the others the companion cells (antheridia), though the actual passage of protoplasm from the latter into the former was not seen. Other forms are found with resting sporangia quite like those of Olpidiopsis but without an antheridium, and Schröter (in Engler and Prantl) restricted the genus Olpidiopsis (in Olpidiaceæ) to these species with (presumably) asexually produced resting sporangia, transferring to a new genus Diplophysa (in Oochytriaceæ) those species with sexually produced sporangia (Olpidiopsis spp. and Pleocystidium). Barrett (1912) rejects the name Diplophysa in favour of Olpidiopsis, using the name Pseudolpidium for the forms with Olpidiopsis-like but asexuallyformed resting-sporangia (Fig. 6, C). Barrett studied three species of Olpidiopsis (Fig. 6, E) in detail, and found two cilia of equal length attached at or near the anterior end of the elongated zoospore, which showed two motile stages separated by a brief rest-period; the individuality of the zoospore after entering the host is maintained throughout development, no plasmodium being formed, and apart from slight amoeboid movement immediately after entrance the parasite does not undergo any noticeable changes of form; segmentation of the sporangial contents occurs at least in part before the sporangium enters into a resting period and is simultaneous throughout; true sexuality probably exists and takes place by fusion of two sexually differentiated individuals and the subsequent passage of the protoplasm of the smaller male into the larger female cell, followed by fusion of nuclei; the gametangia, like the sporangia, are multinucleate, as is the oospore; germination of the oospore was unfortunately not observed in any of the species.

As Barrett points out, these Olpidiopsis forms may be regarded as primitive sexual organisms of the Oomycete type, as indicated by the influence of external conditions on the development of the sexual stage, the mode of fertilisation, the unequal size of the two gametes, and the apparent morphological equivalence of these gametes with the sporangia. The cytology of the Pseudolpidium forms is not known, but in view of the conditions found in Reessia, Monochytrium, Olpidium and the closely related Olpidiopsis, it seems probable that a sexual process occurs also in these forms. In any case, we have in the Olpidiaceæ a remarkably interesting series leading from primitive types like Reessia and Monochytrium up to definitely oogamous forms and thence, as we shall see later, to

the Peronosporaceæ, probably through the Ancylistineæ.

(To be continued).

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CARBON ASSIMILATION.

A REVIEW OF RECENT WORK ON THE PIGMENTS OF THE GREEN LEAF AND THE PROCESSES CONNECTED WITH THEM.

By Ingvar Jörgensen and Walter Stiles.

(Continued from p. 250).

B. THE CHEMISTRY OF CHLOROPHYLL.

Chlorophyll is a neutral substance which on treatment with alkalis yields salts of acids which are known as chlorophyllins. These salts of the chlorophyllins are soluble in water and are also green in colour like chlorophyll. In the production of chlorophyllins, a group which was bound to an acid radicle, has been split off from the chlorophyll molecule, that is, the chlorophyll has undergone saponification like an ester.

The chlorophyllins which are formed by alkaline hydrolysis from alcoholic extracts of leaves are easily decomposed. They were, however, isolated by Willstätter, and were found on analysis to contain magnesium, which was bound to the nitrogen in a complex way. The magnesium cannot be electrolytically dissociated as in a magnesium salt. The magnesium containing group is very easily affected by acids, but is stable in presence of alkalis.

On heating chlorophyllins with concentrated alcoholic alkalis, a series of decomposition products, phyllins, are obtained by removal of carboxyl groups, until in the final phyllin only one remains. The phyllins are also acids containing magnesium. On removal of the last carboxyl group a substance devoid of oxygen, ætiophyllin, is produced, having the composition $C_{31}H_{34}N_4Mg$, in which also the magnesium is bound to the nitrogen.

If mineral acids and acetic acid are allowed to act on the phyllins, these lose their magnesium. The series thus obtained

from the phyllins by the action of acids are called porphyrins. Thus ætiophyllin gives ætioporphyrin, $C_{31}H_{36}N_4$.

While the action of alkalis on chlorophyll produces no change in the optical properties of the chlorophyll derivatives, with acids the colour becomes olive-green and the fluorescence becomes less. It is another group of the chlorophyll that is attacked, but the resulting substance is incapable of forming salts: no saponification has taken place.

For instance, the action of oxalic acid or dilute alcoholic hydrochloric acid on an alcoholic extract of leaves is to produce a wax-like chlorophyll derivative called phæophytin. It contains no magnesium, and the replacement of that metal by hydrogen is the only change which takes place. The substance is not easily soluble in alcohol and so is precipitated easily. Its solution differs from that of chlorophyll in colour, but if a metal is introduced into the molecule again, it regains the chlorophyll colour. This may easily be effected with copper and zinc by adding their acetates to phæophytin. Magnesium is not so easily replaced, but Willstätter has succeeded in doing this by treating phæophytin with magnesium methyl iodide.

If phæophytin is saponified with alkali, nitrogen-containing acids are produced and a nitrogen-free alcohol called phytol of the formula $C_{20}H_{39}OH$. Willstätter has also shown that a—COOCH₃ group is broken up by this hydrolysis.

From the results of the treatment of chlorophyll with alkalis and acids Willstätter has thus been able to write the formula of chlorophyll a as $(C_{32}H_{30}ON_4Mg)$ (COOCH₃) (COOC₂₀H₈₉), that of chlorophyll bas $(C_{32}H_{28}O_2N_4Mg)$ (COOCH₃)(COOC₂₀H₃₀).

When a mixture of chlorophyll a and b is saponified with alkali the green colour changes first to a deep brown (chlorophyll a changes to yellow, chlorophyll b to red). After a few minutes the colour changes back to the original green. Willstätter explains this as possibly due to the presence of a lactam ring CO—NH which is opened when the brown phase is produced.

The reappearance of the green colour is supposed to be due to the formation of another lactam ring which is more alkali-stable.

During the production of the brown phase the complex combination of the magnesium is affected. On the reproduction of the green colour the carboxyl group might combine with the same nitrogen group or with a different nitrogen group, or the nitrogen might combine with another carboxyl group.1

From the formulæ of chlorophyll given above it will be observed, that the phytol component amounts to one-third of the weight of the chlorophyll.

Now analysis of chlorophyll from different plants gave very various numbers for the phytol content, and plants yielding chlorophyll containing very little phytol were found to be excellent material from which to isolate chlorophyll in a crystalline form. According to Willstätter and Stoll the chlorophyll in plants is accompanied by an enzyme chlorophyllase, active in alcoholic media, which brings about the replacement of the phytol of the chlorophyll molecule by alcohol, so that one gets alcoholysis of the chlorophyll. The substances so produced were known formerly as crystalline chlorophyll. They constitute a group called chlorophyllides. Ethyl chlorophyllide (crystalline chlorophyll) is produced according to the equation

$$\begin{array}{lll} (C_{32}H_{80}ON_4Mg) & (COOCH_3) & (COOC_{20}H_{89}) & + & C_2H_5OH = \\ C_{20}H_{39}OH & + & (C_{32}H_{30}ON_4Mg) & (COOCH_3) & (COOC_2H_5). \\ & & \text{Phytol.} & \text{Ethyl chlorophyllide.} \end{array}$$

Similar chlorophyllides are produced with other alcohols.

Of much interest is the manner in which the presence of two chlorophylls in leaves was discovered. It has been mentioned already that the treatment of an alcoholic extract of leaves with dilute acid yields a wax-like substance called phæophytin. It was observed by Willstätter that the decomposition of phæophytin results in a considerable number of products, but that these consist of two distinct groups, one called the phytochlorins which are olivegreen in solution, and another group, comprising those which give solutions of a beautiful red colour, called phytorhodins. These compounds were so numerous that they were simply differentiated by letters so that they were designated phytochlorin a, phytochlorin b, etc.

The method by which they were separated by Willstätter and Mieg (1906) is based on the different distributions of these substances between ether and hydrochloric acid. The concentration of the hydrochloric acid determines how much of the substance is extracted by it from ether. Thus only traces of phæophytin a are extracted

In alcoholic solution chlorophyll undergoes a change which Willstätter calls allomerisation. He supposes the lactam ring is opened and another lactam ring formed. Such allomerised chlorophyll does not give the brown phase. This change does not take place in ether or chloroform solutions. It is accelerated in alkaline solutions but inhibited by small quantities of acid. Therefore, in the separation of the two chlorophylls, a small quantity of oxalic acid is added. See section D (6), p. 292.

from an ether solution by an equal volume of 25% hydrochloric acid, while with 32% it is almost entirely extracted: again only traces of phytochlorin e are extracted by 0.5% acid, but it is almost entirely extracted with 4 to 5% acid. The "hydrochloric acid number" is the percentage content of that acid which by shaking removes approximately two-thirds of the dissolved substance from an equal volume of an ethereal solution.

It was thus possible to separate the decomposition products of phæophytin by fractionating the mixture of them in ether with hydrochloric acid of different concentration.

The formation of the large number of decomposition products of phæophytin is due to the instability of chlorophyll in alcoholic solution. By uniform treatment of material, however, Willstätter has been able to ensure obtaining only two, but never fewer, decomposition products from phæophytin: phytochlorin e, $C_{32}H_{32}ON_4(COOH)_2$, and phytorhodin g, $C_{32}H_{30}O_2N_4(COOH)_2$.

As the molecular weight of phæophytin is of the same order of magnitude as that of phytochlorin e and phytorhodin g, and as these cannot be converted into one another, and as moreover they are formed in definite proportions by weight, it follows that they are formed from two different phæophytins and ultimately from two different chlorophylls.¹

The summary opposite may serve to make clear the action of different reagents on the chlorophyll molecule. In each case we have represented the actions with chlorophyll a. Similar reactions take place with chlorophyll b.

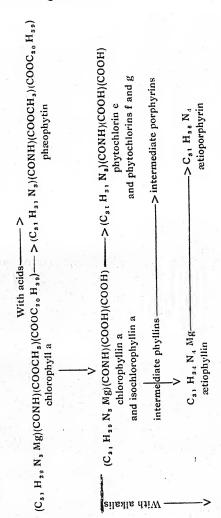
Description of Chlorophyll. Chlorophylls a and b as precipitated out by petrol ether are microcrystalline. Chlorophyll a forms a blue black powder which makes a green mark. Chlorophyll b forms a green to green black powder.

Chlorophyll a is easily soluble in ethyl alcohol, acetone, chloroform, ether and carbon-disulphide, pyridin and benzene, moderately soluble in methyl alcohol and soluble with difficulty in 80% ethyl alcohol, 90% methyl alcohol (even warm) and petrol ether (even warm). It is practically insoluble in 80% methyl alcohol.

Chlorophyll b has much the same solubility properties as chlorophyll a, except that the solubility is generally slightly less. It is completely insoluble in petrol ether and practically insoluble in 90% methyl alcohol.

¹ For further information on the chemistry of chlorophyll see Willstätter and Stoll (1913). A short account of the chemistry of chlorophyll has also recently been published by Willstätter in English; see Willstätter (1915).

The ethyl alcoholic solution of chlorophyll a is blue green with deep red fluorescence, the colloidal solution in water is pure green and does not fluoresce. The alcoholic solution of chlorophyll b is greener, compared with a it is tinted a little yellow and the fluorescence is red with a tinge of brown.



The different behaviour of the two chlorophylls on saponification has been mentioned previously. Chlorophyll a gives a pure yellow and b a red colour both of which change back subsequently to green.

C. THE YELLOW PIGMENTS.

Although the yellow pigments may have physiological importance in carbon-assimilation there is not much to be said in regard to their chemistry. They both give non-fluorescent yellow solutions stable in alkaline but very easily dissociated in acid media.

Carotin is identical with the yellow pigment of carrots. It is an unsaturated hydrocarbon of the formula $C_{40}H_{50}$ crystallising in rhombohedra with a lustrous blue surface, but appearing red in transmitted light. It is easily soluble in chloroform, carbon-disulphide and benzene, soluble with difficulty in petrol ether and ether, and in even boiling methyl and ethyl alcohol; in the cold it is almost insoluble.

Characteristic of it is its distribution between petrol ether and methyl alcohol. If to a solution in petrol ether is added methyl alcohol containing a little water, the alcohol layer remains colourless.

It undergoes auto-oxidation. If it stands in air it becomes bleached and increases in weight by 35% in dry air and by 41% in moist air. With the halogens it forms addition compounds.

It gives a red solution in carbon-disulphide and a deep blue solution in concentrated sulphuric acid.

Xanthophyll has the formula $C_{40}H_{56}O_2$. The crystals are pleochromatic often with a steel blue lustre. In transmitted light they are yellow and only red where two or more cross one another and in this way are easily distinguishable from those of carotin although the colour of the two pigments in solution is very similar. The behaviour of xanthophyll with sulphuric acid and halogens is the same as that of carotin. It is insoluble in petrol ether, the solvent is not even coloured; in methyl alcohol it is soluble with difficulty but more easily than carotin. It is also soluble with difficulty in carbon-disulphide. In ether it is more soluble, and is easily soluble in chloroform. Like carotin it undergoes auto-oxidation and a solution of xanthophyll bleaches in presence of air very quickly, much quicker than carotin.

If a xanthophyll solution in methyl alcohol is mixed with petrol ether and a little water added, the greatest part of the pigment remains in the methyl alcohol layer.

Although carotin and xanthophyll give very similar solutions it is difficult to compare the colour intensities of the two because the colour varies with the solvent and the concentration. The carotin is always stronger and in dilute solutions they are not comparable because the shade varies.

The alcohol solution of carotin or xanthophyll has a spectrum with one band in the blue and another in the indigo blue and the end absorption commences in the violet. The bands in the case of xanthophyll are displaced a little towards the violet as compared with carotin.

In carbon-disulphide solutions the difference between the two spectra is greater, and the absorption bands are displaced towards the red end as compared with those in alcoholic solution.

- D. THE EXTRACTION AND PREPARATION OF THE PURE PIGMENTS FROM THE LEAF.
- (1) The Choice of a species. In obtaining the pigments of the leaf in the free state it is obvious that the first question to arise is the choice of material from which the pigment should be extracted. This question immediately resolves itself into two: firstly, the choice of a species on which to work, and secondly, the preparation of the leaves for treatment with the solvent.

In regard to the choice of a species, Willstätter divides plants into two groups. (i) Those rich in the enzyme chlorophyllase, which on extraction of the pigment give the substance known as "crystalline chlorophyll" (chlorophyllides). In this group are hogweed (Heracleum sphondylium), hempnettle (Galeopsis Tetrahit) and the hedge woundwort (Stachys sylvatica). (ii) Those poor in chlorophyllase, which on extraction of the pigment give true chlorophyll. Of the plants in this group Willstätter recommends for use the nettle (Urtica sp.) which is very abundant, is rich in chlorophyll, and poor in enzymes. Nettles are easily dried and when dried they keep well. They have the disadvantage that in the process of extraction the chlorophyll is easily altered, but this disadvantage can be obviated by quick preparation.

It is interesting, as Willstätter points out, that as long ago as 1852, G. G. Stokes proposed the use of nettles as a source of chlorophyll.

(2) The Preparation of the Leaves. The earlier preparations of chlorophyll were nearly all made by boiling fresh leaves in alcohol, and for this purpose, on account of its abundance, grass was very commonly used. Sometimes the fresh leaves were first boiled with water, after which the pigment could be extracted with warm alcohol. Hoppe-Seyler first treated the leaves with ether in order to extract the waxes, before extracting the pigment with boiling alcohol.

Willstätter first dried his leaves and powdered them before extracting the pigment. The advantages and disadvantages of using fresh and dried leaves may be summarised as follows. Preparations from fresh leaves are important (i) for analytical purposes when small quantities only are necessary; (ii) when it is necessary to find the true proportions of the various pigments; (iii) when the action of chlorophyllase on chlorophyll is utilised for the preparation of crystalline chlorophyll. On the other hand fresh leaves have the disadvantages that (i) they are more difficult to divide finely; (ii) it is more difficult to prevent the alteration of the chlorophyll in fresh leaves than in the dry powder. However, this difficulty may be overcome by treating with a watery solution of methyl or ethyl alcohol of such concentration that no chlorophyll is extracted while at the same time the enzymes are destroyed.

Willstätter himself used the dried powder of leaves for all ordinary extractions. The use of the dried powder has these advantages. (i) To obtain the same quantity of pigment a much smaller quantity of material is required than if fresh material is used. This allows of the use of small vessels for the extraction operations, a very important advantage when the small quantity of chlorophyll present in the crude material is considered. (ii) A saving in the solvents is effected. These are not diluted by the water content of the leaves which constitutes about 75% of the fresh leaves. (iii) As a leaf can be chosen the dried powder of which keeps well, the preparation of the pigments can be made independent of the season and growing place of the plants.

The disadvantages of using the dried material are as follows:
(i) Loss of chlorophyll owing to drying. If the drying is done properly this loss is very small. Thus Willstätter found in alcoholic extracts of dried nettle and of Galeopsis 95 to 96% of the chlorophyll in fresh leaves. (ii) Again, if the leaves are not properly dried, alteration of the pigments may take place. Some dried leaves are spoilt by being kept (e.g., Grass), others (e.g., Elder and Conifer leaves) are even spoilt by drying. But even in such cases the chlorophyll may be preserved unchanged if the leaves are dried in a vacuum desiccator over sulphuric acid.

It should be mentioned that Willstätter has compared the pigments extracted from fresh leaves and dried leaf powder and has found them identical.

(3) The Solvents. For the various reasons given above Willstätter used the dried powder of nettle leaves for all ordinary

extractions of chlorophyll. Now it has already been pointed out in an earlier section of this chapter that the efficiency of a solvent for extraction is not necessarily conditioned by the solubility of extracted chlorophyll in it. Thus pure extracted chlorophyll is easily soluble in benzene, in petrol ether and in water-free acetone, as well as in alcohol, ether, and carbon-disulphide, yet chlorophyll is only very slowly extracted from dried leaf powder by pure alcohol, ether and acetone, and not at all by benzene, petrol ether and carbon-disulphide. On the other hand it is immediately extracted by methyl alcohol.

The foundation then of Willstätter's method of extraction is the use of solvents containing a moderate content of water. This latter forms a salt solution with some of the cell contents, and this salt solution effects an alteration in the condition of the chlorophyll which thus becomes easily soluble in the organic solvent. If the solvent contains the correct water-content the pigment is almost entirely extracted. The pure solvents are effective in the order, methyl alcohol, acetone, ethyl alcohol, ether. When 1% water is added, acetone, ethyl alcohol and methyl alcohol are all equally effective as solvents. With a higher water-content acetone is better than any of the others. The best solvent is acetone containing 15% (by volume) of water. Willstätter however, uses 80% acetone, because with this somewhat higher water-content, a quantity of accompanying substances are not extracted and the separation of the pigments becomes easier. If alcohol is used for chlorophyll extraction the most satisfactory solvent is one containing 10% (by volume) of water.

The earlier extractions of chlorophyll were always made with hot or at least warm solutions. All Willstätter's extractions have been made in the cold, i.e., at ordinary laboratory temperature, thus preventing any alteration in the pigments which might take place with rise of temperature.

(4) The Method of Extraction of the Pigments. The nettle leaves having been collected, their stalks are removed and the leaves dried at air temperature. They are then powdered as finely as possible, and the resulting powder then dried at a temperature of 30°C. to 40°C. A quantity of this powder, say 500 grams, is then put on a filter paper in a Buchner funnel 24 cms. in diameter and sucked to it by means of a strong water pump, or better, by a vacuum pump. Half a litre of solvent is now allowed to permeate the powder on the filter paper for five minutes without the use of

¹ The quantities of material and reagents and the dimensions of apparatus quoted in this and succeeding sections are those given by Willstätter and Stoll (1913).

the pump. Then 250 c.c. of solvent is added and slowly sucked through with the pump. After five minutes another 250 c.c. of solvent is added and sucked by the pump for ten minutes. This operation is repeated with two further additions of 250 c.c. of solvent, and finally the pump is allowed to work as strongly as possible and the powder is sucked dry. The 1,500 c.c. of solvent used gives 800 to 900 c.c. of extract. It will be noticed that the solvent only passes once through the powder, and that the extraction is rather rapid.

In order to obtain good results with small quantities of solvents in so short a time, a good deal of care is necessary. It is essential to have the powder dry and to get it sucked into a coherent mass on the Buchner funnel before commencing the extraction. The layer of powder on the funnel must not be too high: not more than 5 cms.

The amount of solvent required and the time necessary for extraction depend on the chlorophyll content and on the fineness of the powder, but at the end of the extraction the powder should remain colourless or coloured only slightly yellow.

(5) The Separation and Purification of Chlorophyll. Various methods for the separation of the green pigments have been worked out by Willstätter and his co-workers. The most successful of these, of which we give a résumé below, is that of Willstätter and Stoll.

The essentials of this method are, firstly, the transference of the pigment from acetone to petrol ether and the removal from the petrol ether solution of accompanying substances by washing with watery acetone. The xanthophyll is then removed by means of methyl alcohol. By washing the petrol ether solution with water, the last traces of acetone and methyl alcohol are removed. As chlorophyll is insoluble in pure petrol ether, it is precipitated, and so is filtered from the carotin which remains in solution.

The details of the method are as follows. The extract from 2 kilos of nettle powder is obtained as indicated in the preceding section. Four litres of petrol ether (S.G. 64 to 66) are put in a 7-litre separating funnel and the extract added to this in two successive portions. With each of these additions is also added 1-litre of water, and the funnel is gently rotated at the same time. The liquid separates into an upper deep green layer and a lower weak yellow green layer. The latter is run off. The remaining petrol ether layer is mixed with two successive litres of 80% acetone which removes impurities but very little chlorophyll. The acetone

is then removed by adding 4 successive ½-litres of water, with gentle rotation of the liquid and running off the lower layer each time. (The first time 0.6 litre of acetone is removed and in successive removals 0.5, 0.4 and 0.2 litre). In the acetone thus removed are many of the impurities accompanying chlorophyll in the crude extract.

From the solution remaining, the xanthophyll is first separated by shaking the solution with 3 successive additions of 2 litres of 80% methyl alcohol. After each addition and shaking, the methyl alcoholic layer is removed, and if the last extract is still considerably yellow, one or two further additions of methyl alcohol are made. From these methyl alcohol extracts xanthophyll is prepared.

From the petrol ether solution, which should now have a volume of 3.6 litres, the last traces of acetone and methyl alcohol are removed by washing with water four times, each time using 2 litres of water. With the disappearance of the last parts of the acetone and methyl alcohol, the chlorophyll is precipitated as a suspension from the petrol ether, which thus loses its fluorescence.

This suspension in petrol ether is shaken with some fused sodium sulphate and about 150 gms. of talc, and then filtered through a layer of talc on a Buchner funnel. From the filtrate carotin can be isolated as described later.

The talc and chlorophyll on the Buchner funnel are washed with ordinary petrol ether until this runs off yellow in colour, and then the washing is completed with 300 c.c. petrol ether of B.P. 30° to 50°C. The talc is then sucked completely dry with the pump, and the chlorophyll in it dissolved in pure ether. The ether solution of chlorophyll so obtained is filtered through fused sodium sulphate, concentrated to 100 c.c., filtered twice more, and evaporated to 25 c.c.

From this solution the chlorophyll is precipitated by the slow addition of 800 c.c. of low B.P. petrol ether. The precipitate so obtained may be a blue black powder easily filtered, or it may be so fine that it has to be filtered on talc.

The precipitate is again dissolved in ether, and the solution concentrated to 20 c.c. and dried in a dish in a desiccator.

The pure chlorophyll so obtained consists of about 13 grams (i.e., 6.5 grams per kilo of dried leaves of mixed chlorophyll a and chlorophyll b) forming a thin shining steel blue crust. The yield is about 75% of the total chlorophyll content of the leaves.

(6) The Separation of the two Chlorophyll Components from one another. Although no doubt for many plant physiological purposes it will be sufficient to extract a mixture of the pure chlorophyll pigments, yet in other cases it will doubtless be of the first importance to obtain the two chlorophyll components isolated from one another. In order to make this review as complete as possible we have therefore thought it worth while to give Willstätter's method of separation of chlorophyll a and chlorophyll b in spite of its laboriousness.

The principle involved in the separation is that of the distribution of the two components in petrol ether and methyl alcohol. In a mixture of these two solvents the a component goes to the petrol ether, the b to the methyl alcohol.

Eight grams¹ of chlorophyll isolated according to the method described in section 5 are dissolved in 150 to 200 c.c. of ether, and filtered into a 7-litre separating funnel containing 4 litres of petrol ether (S.G. ·64 to ·66). The chlorophyll begins to precipitate out, and 50 to 100 c.c. of methyl alcohol are added to clear it again.

Before separating the components by fractionation the ether is first removed by washing with 2 litres of 80% methyl alcohol once or twice.

The chlorophyll b is now separated by repeated extractions (14 of them) with 2 litres of 85% or 90% methyl alcohol. The component a remains in the petrol ether. The methyl alcohol must first be saturated with petrol ether (5.5% and 10% respectively is required for this) and immediately before use it must be acidified with 01 gram oxalic acid per litre.

(7) Purification of Chlorophyll b. The first methyl alcohol extract is brought to a concentration of about 90% by the addition of a litre of methyl alcohol. It is washed with a litre of petrol ether, separated from it, added to 2 litres of ether and mixed with much water, by which means the chlorophyll b is brought into ethereal solution.

The second methyl alcohol extract is similarly mixed with a litre of methyl alcohol. It is shaken with the washed petrol ether of the first extract to which has been added another $\frac{1}{2}$ -litre of petrol ether. The solution containing component b is separated from the petrol ether and added to the ether solution of the first extract to which another $\frac{1}{2}$ -litre of ether is added.

Each of the petrol ether portions used in washing is freed by See note on page 289.

means of water from its methyl alcohol, whereon the pigment in it is precipitated.

The third and fourth and fifth alcohol extracts are similarly treated. The content of component b is now considerably reduced.

The sixth methyl alcohol extract is treated with 900 c.c. methyl alcohol, and each successive extract with 100 c.c. less, so that to the 14th extract only 100 c.c. methyl alcohol is added.

These extracts are cleaned in pairs with 1 litre of petrol ether, for the second of each pair a further 1-litre of petrol ether is added.

All extracts thus cleaned are added to the same ether solution which is increased by continual additions of ether, beginning with 1 litre, and decreasing in amount to about ½-litre with the 10th extract.

A 15th and 16th extraction with methyl alcohol is made in order to free chlorophyll a from the last traces of chlorophyll b.

The chlorophyll b solution is now freed from methyl alcohol by washing with water, it is dried with sodium sulphate and evaporated to 500 c.c., and then to 30 or 40 c.c. in vacuo.

The chlorophyll b is then precipitated by the addition of 300 c.c. petrol ether of B.P. 30° to 50°C. and filtered on talc. The filtrate contains much chlorophyll a. It is purified by solution in ether and precipitation with petrol ether, which is repeated several times. It is finally filtered and dried in a vacuum desiccator.

(8) Purification of Chlorophyll a. The petrol ether solution, from which the last traces of chlorophyll b have been removed as indicated in the preceding section, is further purified by shaking it three times with 2 litres of 90% methyl alcohol.

The methyl alcohol is removed and the petrol ether solution of chlorophyll a is washed with water until the chlorophyll is precipitated in quantity. Tale is added to the extent of from 30 to 100 grams, and the whole filtered on a layer of tale on a Buchner funnel. The petrol ether should then run off colourless.

The talc is washed with petrol ether of low B.P. and sucked dry with the pump till all petrol ether smell has disappeared. It is then transferred to a bottle and shaken with as little ether as possible. On filtration on a small Buchner funnel the beautiful deep blue ether solution of chlorophyll a runs through. The chlorophyll and talc are completely freed from one another by further filtration.

¹ The large quantities of ether are necessary because the watery methyl alcohol dissolves much ether and the petrol ether which separates out on dilution makes it difficult to carry the chlorophyll over from methyl alcohol to ether.

Finally the ether solution is concentrated by evaporation and the concentrated solution put in a dish in a vacuum desiccator. On complete removal of the ether, the chlorophyll a is left as a blue black mass.

(9) Purification of Xanthophyll. To the extract containing xanthophyll obtained as described in section 5,4 to 5 litres of ether are added and a quantity of water. Any chlorophyll b that may be present is removed by saponifying it to chlorophyllin by shaking with 30 to 50 c.c. of methyl-alcoholic potassium hydrate. The chlorophyllin is removed by repeated washing with water.

The ether solution of xanthophyll is dried with sodium sulphate, evaporated to 30 c.c., and 200 to 300 c.c. methyl alcohol added. Complete removal of the ether is effected by evaporating down further and filtering the hot solution. On cooling, xanthophyll is deposited in the form of crystals forming shining plates. Water may be added to make the separation of the xanthophyll complete. The yield of xanthophyll from 2 kilos of dried nettle leaves is 0.8 gram.

(10) Purification of Carotin. The carotin is easily obtained. The extract containing it, obtained as indicated in section 5, is evaporated in vacuo at 40°C., and the oily residue treated with 300 c.c. of 90% alcohol. The carotin begins to separate out immediately in shiny steel blue crystals. Crystallisation is complete on standing in the cold.

Any colourless impurity present in the crystalline mass is dissolved in petrol ether. 200 to 300 c.c. of this are therefore added and the carotin filtered from it. The purification is completed by treatment with a mixture of two parts of petrol ether to one part alcohol. The result is a yield of 0.25 gram of carotin from 2 kilos of dried nettles.

(To be continued).

IS PELVETIA CANALICULATA A LICHEN?

By A. Lorrain Smith, F.L.S., and J. Ramsbottom, M.A.

IN intellectual as well as in spiritual matters we are apt to take much for granted until some question suddenly make us halt and give an account of the faith that is in us. A startling suggestion as to the nature of lichens has recently been made with regard to the well-known alga Pelvetia canaliculata. In the present volume of the New Phytologist (pp. 33-42), Prof. G. K. Sutherland describes four new species of Pyrenomycetes inhabiting the thallus of this common brown seaweed. Concerning one of them, Mycosphærella Pelvetia, he states that the very slender intercellular mycelium permeates every portion of the thallus, branching freely and forming a loose net-like web surrounding the cells, but apparently doing "not the slightest trace of injury to the host." The mycelium penetrates into the young receptacles of the alga and there commences to fruit. As the ascospores are set free at the same time as the oospheres, the fungus is enabled to continue the association and to find its way into the intercellular spaces at a very early stage of the development of the alga. Examination of Pelvetia from different parts of the country, and from herbarium specimens, showed that the fungus seems to occur in every thallus. The author states that this "symbiotic species is of special interest as its occurrence throws a new light on Pelvetia, opening the question whether it should be regarded as a lichen rather than an alga." Without entering into the question as to whether the fungus which lives in the mucilage layers of the cell walls of the alga and is practically restricted in its fruits to the presumably more richly nutrient region of the neighbourhood of the algal conceptacles, is in truly symbiotic association with the alga, and assuming the author's view to be correct, can the compound organism Pelvetia-Mycosphærella be placed in the class Lichenes? Or, in general, must every case of symbiosis between a fungus and an alga be considered a lichen? Tournefort (Elémens de botanique, 1694) was the first to classify lichens as such, and systematists since his day have always been clear as to which organisms should be placed in the group. It is true that there are difficulties in some cases as to whether certain species should be placed amongst lichens or fungi, just as at times there is difficulty in deciding between fungi and 1 Loc. cit., p. 34.

alge. From a comparatively early date the lichen gonidia have been recognized as similar to algae growing in the open, but many lichenologists have held in the past that such algæ were free living gonidia, a view again seriously set forth in a recent paper by Elfving.1 Most botanists, however, accept the dual nature of lichens as proved beyond dispute and in the lichen the algæ as well as the fungi are equally concerned in the life of the plant. It is the fungus portion of the plant which produces the fruit and for that reason since lichens, as other plants, are classified on their reproductive structures which necessarily resemble fungi, some writers have suggested distributing lichens amongst fungal families according to affinities: but the algal constituent is also of importance in classification as it frequently determines the form of the thallus and can in no system be ignored. Hence the lichens are the most complicated class of the vegetable kingdom from a systematic point of view. It seems clear that lichens have been evolved on several lines from fungal ancestors: in fact, if Basidiolichens be included in the class there can be no doubt of it. Is such a polyphyletic group a natural one? It seems to us that an account of their structure and physiology, the lichens are just as natural a class as are their nearest relatives the fungi and the algæ, which according to present orthodox theories are also polyphyletic. In any other scheme of classification it would seem to be necessary to go along the theoretical evolutionary lines rather than to group the organisms according to the status they have reached, and though theoretical classification on the lines of very hypothetical phylogenetic trees would doubtless provide an inexhaustable series of interesting exercises, it would not be more scientific than the present grouping and would add greatly to the difficulties of placing individual plants. Can the dual organism Pelvetra-Mycosphærella he placed in this polyphyletic class? It has long been known that certain brown algæ have fungi parasitic in their thalli. For instance, Mycosphærella Ascophylli2 has hyphæ which traverse the tissue of Ascophyllum nodosum in all directions and would appear to form a similar association with the alga, since Cotton states that in spite of the very abundant mycelium the hostplant remains quite uninjured, and that infection appears to take

¹ Untersuchungen über die Flechtengonidien. Acta. Soc. Sci. Fenn. Helsingfors, xliv, No. 2 (1913).

² Church, A. H. A Marine Fungus. Ann. Bot. vii, p. 399 (1893). Cotton, A. D. Notes on Marine Pyrenomycetes. Trans. Brit. Mycological Soc. iii, p. 92 (1909).

place at a very early stage. Judging from the number of fungi which have been recorded on seaweeds (fungi which have, however, received little attention) such endophytic species are probably far from rare.

In considering this special case, it may be well to give a recent definition of the class Lichenes as it is accepted by systematists.1 "Lichenes (Flechten, Flechtenpilze), Ascomyceten und Basidiomyceten, welche mit Arten der Schizophyceæ oder Chlorophyceæ. namentlich der Protococcaceæ und Pleurococcaceæ derart verbunden sind, dass sie auf den Algen entweder nur parasitisch vorkommen oder aber mit denselben eine innige Vereinigung, ein symbiotisches Konsortium, bilden, das eigenartige, bei den Pilzen nicht vorkommende Wachstums- und Lebenserscheinungen zeigt " It is obvious that Pelvetia with its attendant fungus cannot enter into the class as thus defined. No lichen is known which has a brown algal gonidium. Further, there is in Pelvetia a definite and characteristic sexual reproduction, whereas the algæ functioning as gonidia, have never been known to reproduce in any way but by cell-division, though some of the species when living free, reproduce by zoospores, etc. Moreover, the vegetative structure, as well as the reproductive, of the Pelvetia-Mycosphærella complex is totally different from anything known in lichens. If the association be regarded as a lichen as the author suggests to what are we led? The association would be the type of a new division of lichens and would rank as Phæolichens. The gonidia of lichens are also free living plants and so can be placed in the algal families to which they belong. The Pelvetia-Mycosphærella association is so close that the author has not yet found an uninfected alga and therefore on the assumption that "symbiosis" between alga and fungus implies a lichen, "Pelvetia" would have to be taken out of the Fucaceæ, as it is never free-living—a reductio ad absurdum.

It seems to us to be not a question of whether Pelvetia-Mycosphærella is to be considered as a lichen but what relation exists between the two plants. If it be really a case of symbiosis, it seems to be more akin to mycorhizæ, although the Ustilagineæ with their eventual spore formation are at present more suggestive. No one has yet proposed forming special classes for mycorhizal phanerogams, pteridophytes or hepaticæ even in those cases where the whole plant is permeated by a non-fruiting fungus as in Ericaceæ, Lolium, etc., and where the association seems to be an ¹ Engler (-Gilg) Syllabus der Pflanzenfamilien, Editn. vii, p. 67 (1912).

obligate one for the higher plant. The association under discussion, if symbiotic, appears to us to be of this kind and not one with the peculiar structural and physiological characteristics of lichens. It would be exceptionally interesting to find that there is an obligate symbiosis in this case (also in other species of the alga) and we hope that Mr. Sutherland's further investigations will throw light on the point.

It may be pointed out in conclusion that if the most recent "biological" definition of a lichen be adopted -- "A lichen is a fungus which lives during all or part of its life in parasitic relation with the algal host and also sustains a relation with an organic or an inorganic substratum"—then the association (or rather Mycosphærella Pelvetiæ) is not a lichen. We ourselves are conservative enough to still hold to "the assumption that the alga forms part of the lichen" and do not seek any support for our contentions in such a confused definition. "Writers of text-books on plant morphology" may be interested to know that they "have, with a few notable exceptions, signally failed to be consistent in their treatment of lichens"-a statement which is upheld by the absurd assumption that the authors considered the lichen a fungus or an alga according to which name came first in their definition. In this short note we have necessarily left out of account much that might have thrown more light on the discussion such as the question of symbiosis in lichens including antagonistic- and para-symbiosis. The matters involved will be discussed fully in a forthcoming work on lichens now in preparation by one of us.

¹ Fink B. "The nature and classification of lichens, ii. The lichen and its algal host." Mycologia, V, p. 97, 1913.

TYPE SLIDES.

MATTER which seems to call for some consideration from botanists is the question of the preservation of permanently mounted microscope slides prepared in connection with researches on the anatomy, cytology, etc. of plants. In the case of systematic botany, it seems always to have been more or less customary to deposit type specimens (or co-types) in a public institution or in some other manner to insure that the described plant be not lost to science. It is very surprising that no recognised method of preserving botanical preparations has been adopted (at least in this country) except in the case of fossil botany. It would be exceedingly difficult to trace slides which, say twenty years ago, were at that time considered important enough by the author to describe and figure!

When an investigator has taken the trouble to preserve his slides and has not dispersed them either through change of interests or magnaminity during his life-time, it seems very unusual for him to have made any provision for their passing into proper hands at his death. If figures were perfect and if botanical questions could be finally settled by any one investigator, the matter would be of little importance. The discovery of a new fact may however necessitate the revision of the work of previous authors; and moreover, certain investigations have been made with exceedingly rare plants, and in such cases it is practically impossible to confirm the results published. Further, a slide which has been drawn and described has a certain historical interest.

Would it not be advisable to establish the practice of depositing one or more representative slides which prove or illustrate the author's contentions in some institution? Possibly a bureau of some description might be formed in connection with the British Association for their reception, but probably the logical course would be to place them in the British Museum where already there are collections of slides of historical interest as, for example, those of de Bary. Here they would be easily accessible and available for examination by any responsible and reputable person at the discretion of the officer in charge of them. A statement that such a slide, or selection of slides had been presented to a national, or other, collection could be made by the author on the publication of his work.

J. RAMSBOTTOM.

ERNEST LEE.

Ernest Lee was killed in the trenches of the Western Front, on July 10th, 1915. He was born at Stanley Cross End, Yorkshire, on April 11th, 1886, but spent most of his childhood at Burnley, where his parents took up their residence. It was at the evening classes of the Burnley Technical Institute that he was first able to get lessons in natural science. Those who learn the elements of science under such conditions must have some grit to carry on. In 1906, Lee obtained a National Scholarship in Geology and went to the Royal College of Science. There he had a successful career, obtaining a first class A.R.C.Sc., the Edward Forbes Medal and Prize in Botany and a Marshall Scholarship in 1909. The last enabled him to stay another year at college and he worked at the Morphology of Leaf Fall on which he published a paper in the Annals of Botany, 1911. In May, 1910, he was appointed Demonstrator in Botany at Birkbeck College and in the following year Assistant Lecturer. It was in the autumn of 1910 that I first met Lee. We became good friends immediately, though we saw little of each other away from the college, except that we went together on occasional botany rambles, to Chelsea Gardens, or, at times, to a music hall. No one could wish for a better colleague: he was ever ready to assist in any possible way he could. He was an enthusiastic lecturer and took endless trouble in preparing work for his classes. The students appreciated him; it was apparent at the time but it was most obvious when the classes returned after the summer vacation of 1913 to find that he had left for the Department of Agricultural Botany at Leeds University. Away from college he was just as enthusiastic and was perhaps at his best on a botanical excursion. Interested in most branches of botany, an excellent field man both from a floristic and an ecological point of view-over lunch and a cigarette he was quite prepared either to "rag" or to talk on sociological or philosophical subjects, showing particular keenness on social problems. He was no mere dreamer but matter of fact, shrewd, and a man of stern and clear convictions, generous, a thorough sportsman with a keen sense of humour. When certain of himself he was indisposed to compromise. and he had a full endowment of the northern Englishman's lust of battle. I have no idea as to what his religious beliefs or politics were: of this I am certain that in any position in which he was

' See also an obituary notice by Dr. H. C. I. Gwynne-Vaughan in Ann. Bot. xxix, p. 639 (1915).

placed he would have remained the true democrat he was in thought and in action: he can be written as one who loved his fellow men.

As a botanist he was only just getting into his stride. Besides the paper on leaf-fall he had published two on seedling anatomy. He was not one of those fortunates who are botanically nursed before going up to a University and then spoon-fed afterwards. He was what he was of his own ability and energy and was rapidly approaching botanical maturity when, after the gradual throwing off of what I imagine were the effects of previous struggles, he would be prepared to give whole hearted attention to some difficult botanical problem.

Just when matters were opening out for him the war commenced. He was always keen on the O.T.C., which he joined on going to Leeds, and was thus able to help in its organization when hostilities broke out, taking charge of the musketry. Loathing war as one of the deadly sins, he was happy in the knowledge that he was "fit": fitness in mind and in body for himself and for others with the opportunity to be so was one of his ideals. Early in Septemper, 1914, he was gazetted to the 4th Duke of Wellington's (West Riding) Regiment. He was made machine gun officer, promoted full lieutenant at the end of the month and was already marked out for further promotion. In November, 1914, he married Miss H. S. Chambers, Lecturer in Botany at Royal Holloway College, and in April, 1915, he went to France. On July 10th a bullet passed through the parapet of the trench and penetrated his head. He died within two hours without regaining consciousness. From letters received he was the same "old Lee" to his men and brother officers that he was to many of us. Whatever hurly-burly might be afoot he was cool, clear, shrewd, courageous, discerning the essence of the situation and master of himself. Ernest Lee gave his life for his ideals.

J. R.

¹ Ann. Bot. xxvi, p. 727 (1912) and xxvii, p. 303 (1914).

THE INTER-RELATIONSHIPS OF PROTISTA AND PRIMITIVE FUNGI.

By F. CAVERS.

(Continued from p. 280).

Another line leading from the lower Olpidiaceæ has probably given rise to certain forms which may be included in Schröter's family Synchytriaceæ; this is distinguished from the Olpidiaceæ by the fact that the body divides up to form a sorus of zoosporangia, As understood here the family instead of a single sporangium. includes six genera-Sorolpidium, Anisomyxa, Rhizomyxa, Rozella, Woronina, Woroninella and Synchytrium. In Sorolpidium (Fig. 6, F) the amœboid vegetative stage is succeeded by the reproductive phase in which the parasite divides into a number of uninucleate amæbæ; these form the spore mother-cells, contained within an enclosing membrane, and after a resting period each nucleus undergoes two mitoses, thus giving rise to four zoospores; Nemec also describes zoosporangia of varying sizes which gave rise directly to zoospores instead of to spore-clusters, and also thick-walled cysts, but the connexion of these with the life cycle of Sorolpidium could not be determined with certainty. In another new genus described by Nemec (1913), Anisomyxa, the vegetative body resembles that of Sorolpidium in being at first uninucleate but later growing so as to fill the host-cell and becoming multinucleate, but here two kinds of sori were found, apparently differing only in the size of the constituent sporangia, the latter being in both cases uninucleate at first and later multinucleate and the zoospores being similar in form. In neither genus was a sexual process observed. In Rhizomyxa, a genus described by Borzi in 1884 and placed by Schröter in the Ancylistineæ but probably better classed with Synchytriaceæ, the amœboid body is evidently similar to that of the genera just mentioned, and after becoming clad with a membrane it divides up into portions each of which may either become at once a single zoospore or may divide further so as to produce numerous zoospores -that is, we may either say that the amorboid parasite produces alternatively zoosporangia and sori, or that both kinds are sori but in the former kind the sporangium produces a single spore. also described in Rhizomyxa thick-walled resting sporangia, which also were formed either singly or as a sorus, and sexual organs like those described for Olpidiopsis, the body dividing into a club-like antheridium and spherical oogonium and the former emptying its contents into the latter by means of a short tube. However, nothing is known of the cytology of Rhizomyxa, and it remains to be demonstrated that the sexual organs described by Borzi really belong to this organism and not to an Olpidiopsis or some other genus. Rozella and Woronina were both described by Cornu and do not appear to have been reinvestigated more recently; in both, the zoospores are biciliate and the sori are loosely arranged from the beginning, that is, the parasite breaks up into completely separate portions not enclosed within a common membrane, each portion developing into a sporangium; Rozella apparently differs from Woronina only in having the sporangia of a sorus arranged in a row instead of a compact cluster. Other imperfectly known formsare Woroninella (Raciborski, 1898) and Micromyces (Dangeard, 1888); the former has polyhedral thick-coated sori and may be said to differ from Woronina mainly by its adaptation to land life and

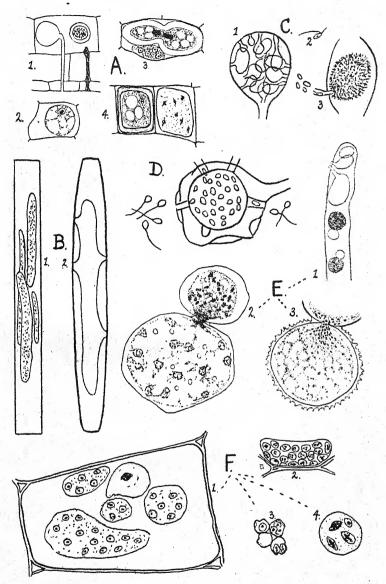


FIG. 6. CHYTRIDIALES. A. Olpidium salicornia: 1, part of section of host showing on the right the remains of an infection-tube and (above) a young sporangium, on the left an empty sporangium with exit-tube; 2, young parasite with one nucleus; 3, above are two amœbæ fusing, below is an amœbæ with four nuclei; 4, on the left a cyst, on the right a parasite undergoing nuclear division. B. Ectrogella bacillariacearum: 1, young zoosporangia in Synedra; 2, empty sporangium with several exit tubes. C. Pseudolpidium sp.: 1, empty zoosporangia in a Saprolegnia hypha; 2, zoospore; 3, spiny-coated cyst with exit-tube. D. Pleotrachelus fulgens: zoosporangium with several exit-tubes, zoospores escaping. E. Olpidiopsis vexans: 1, three empty sporangia and two mature oospores in a Saprolegnia hypha; 2, fusion of antheridium and oogonium (nuclei of antheridium in division, those of oogonium in the resting condition); 3, sexual organs, showing passage of male nuclei into

oogonium, F. Sorolpidium betæ: 1, cell of host showing amæbæ in various stages of growth and nuclear division; 2, young sorus showing nuclear division in the sporangia; 3, part of same more highly magnified; 4, a single sporangium of a sorus, showing nuclear division. A and F from Nemec; B and D from Zopf; E from Barrett.

perhaps from Synchytrium mainly in having biciliate zoospores, while Micromyces has a spiny-coated sorus and appears to differ

from Rozella mainly in having uniciliate zoospores.

The life history and cytology of Synchytrium have been described by various writers, and a monograph of the genus has recently been published by Tobler (1913), so that in many respects it is the best known member of the Chytridiales. The parasite may produce either thin-walled summer sori or thick-walled cysts which remain uninucleate through winter and in spring germinate to form a sorus. In the latter case the division does not occur in situ but after the contents covered by the thin inner coat have burst through the outer coat. In S. taraxaci the cyst divides directly to form zoospores, but in other cases the cleavage which accompanies nuclear division results in the formation of a number (30 to about 250) of sporangia, each of which divides into numerous uniciliate spores. cytology of Synchytrium presents some remarkable features, though there is considerable diversity in the various species investigated, as well as some discrepancy between the accounts given by different writers for the same species. Thus in S. taraxaci the primary nucleus divides by an amitotic process which may be termed nuclear gemmation, masses of chromatin (chromidia) derived from the nucleolus passing into the cytoplasm and becoming organised to form the secondary nuclei, which later divide by mitosis. In S. endobioticum this process is carried still farther, for here the extruded chromidia do not even organise secondary nuclei but pass unchanged into the zoospores, the remains of the primary nucleus persisting unchanged in the centre. Some features in the cytology of Synchytrium appear to have their only parallel among the Protozoa, where chromidial extrusion plays an important part in the organisation of the nucleus, but a careful comparison of the various accounts given hardly supports the view adopted by some authors that Synchytrium is completely isolated from the remaining Chytridiales. According to Nemec, Sozolpidium and Synchytrium are too sharply separated cytologically to be placed in one family, the main difference being that in Sorolpidium the nucleolus of the vegetative nuclei persists and divides directly (though at the same time a spindle is organised as in a typical mitosis) instead of passing into the the cytoplasm and providing material for the formation of the chromosomes as in Synchytrium. A very similar process has been described for the Plasmodiophorales, and it may perhaps be regarded as intermediate between direct (amitotic) division or nuclear gemmation, as seen in some species of Synchytrium, and ordinary mitosis; and in view of the diversity in modes of nuclear division found within the limits of the genus Synchytrium, as well as the fact that there are various reasons for regarding the Chytridiales and Plasmodiophorales as being closely related, the cytological phenomena observed in Sorolpidium and Synchytrium appear simply to indicate that the former genus may be taken as a primitive type of Synchytriaceæ and as connecting this group with the Plasmodiophorales. (To be continued).